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UNIVERSITY OF IOWA STUDIES IN PSYCHOLOGY

No. XVI

EDITED BY

CHRISTIAN A. RUCKMICK

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UNDER THE DIRECTION OF

LEE EDWARD TRAVIS

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PREFACE

The more significant researches in the Psychological Laboratories of the University of Iowa are accumulating so rapidly and their publication through the regular channels of the professional journals would otherwise be so long delayed that we have thought it advantageous to issue several monographs during the current year, even though each one of them is less bulky than any of our recent numbers. This volume is, therefore, the first of a series of three which are to be published this year. It contains three doctorate dissertations completed under the supervision of Dr. Lee Edward Travis, Director of the Psychological Clinic in the University Hospitals. Technically they ought to be considered as of a piece with similar studies published last year in Volume XLIII in this Psychological Monograph series. Dr. Travis is also responsible for the preliminary editing of these studies.

Under a new policy adopted by the Graduate School the papers are necessarily much abridged. But full documentary evidence is obtainable in the several cases through the complete protocols which are on deposit in the Library of the University of Iowa. It has been felt advisable, therefore, not only to educate our graduate students in the matter of writing printer's copy thus eliminating useless verbiage but also to spare them the burden of the high costs of publication.

The editor wishes to seize this opportunity of publicly acknowledging the splendid spirit of coöperation which exists between the several allied branches of the Department of Psychology. In this instance Dr. Travis has displayed his uniformly excellent attitude in conforming his material to the standard requirements of the Iowa Studies in Psychology and in facilitating in many other respects the process of editing these studies. The continued productivity of his clinic in the direction of pure research also deserves favorable commendation.

THE EDITOR

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INTRODUCTION

The present volume continues the practice established last year in the University of Iowa Studies in Psychology, No. XV, of bringing together in one monograph certain studies from the psychology laboratory in the Psychopathic Hospital at the University of Iowa. As was the case in the previous number, the writer is indebted to the editor of the Iowa Studies, Professor Ruckmick, for his kind and expert help in the preparation of the manuscripts for publication.

Two of the investigations included here are outgrowths of previous work from this laboratory. Dr. Lindsley made several approaches to the problem of determining various possible sources of action-current frequencies expressed in the peripheral nerves and muscles. Dr. Nystrom compared the action-current and the muscle-thickening methods for determining reflex response latencies. The third investigation introduced a new technique into this laboratory. Dr. Bender studied the effects of emotion, pain and alcohol upon the photographically determined pupillary reflex activity.

I wish to express my appreciation of the conscientious efforts and serious purpose of those of my students whose contributions make up this issue.

LEE EDWARD TRAVIS

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THE EFFECT OF PAIN AND EMOTIONAL STIMULI AND ALCOHOL UPON PUPILLARY REFLEX ACTIVITY

by

W. RALPH GRIGGS BENDER

I. Introduction. Pupillary phenomena have been investigated from many angles. For both normal and psychopathological cases the size of the pupil and the rate, both of contraction and dilatation, for various intensities of light and under the effects of drugs, emotions and pain have been scrutinized.

The pupil, or the aperture of the iris, has a maximum diameter in the dark and a minimum diameter in strong light. *Blanchard* (3) found the extent to be from 2.0 mm. to 7.5 mm. *Blakesley* (2) maintained that the maximum diameter reported by most investigators was too great. He found such to be between 6.74 mm. and 7.2 mm. It is usually accepted that the pupillary range is from 2.0 mm. under strong light to 8.0 mm. in the dark (47). According to *Cason* (6) and *Reeves* (39, 40), however, normal individuals showed marked variations in the range of the diameter. *Reeves* (40) stated that the size of the pupil of any given individual varied only slightly from day to day. From this it would be inferred that following a period for dark adaptation and subjection of the pupil to a known intensity of light the rate of contraction would not vary to any great extent from day to day. However, *Löwenstein* (29) maintained that the rate of contraction was not consistent. *Blanchard* (3) found that the pupil was constantly fluctuating over a small range when the eye was subjected to a fixed brightness. *Löwenstein* (29) found this to be true also but claimed that there are two types of reaction, namely, (1) a quiet and slow reaction and (2) a rapid and oscillatory reaction which he called the restless pupil.

The pupillary reflex which is an organic, unconscious and

involuntary response possesses certain characteristics (27) (6). One of these is the rate of closing, *i.e.*, from dark adaptation to various brightnesses of light the pupil decreases in size at certain speeds. From maximum dilatation to maximum contraction *Reeves* (39, 40) found the period to be slightly less than 5.0 sec. *Weiler* (46) found similar results while *Gradle* (19, 20) recorded a shorter time. All of these workers used a motion-picture camera to photograph the pupillary changes. Five seconds, however, is usually accepted as the length of time needed for complete contraction of the average pupil (47).

When light is flashed on a normal eye accommodated for the dark, there is a short time before actual contraction begins. This lapse of time between the stimulation and the initiation of contraction is known as the latent period. *Weiler* (46) found this period to vary from .15 to .20 sec.; *Reeves* (39, 40) found it to be .20 sec.; and *Gradle* (19, 20) found it to be .1875 sec. After the latent period there follows a rapid increase in contraction to almost the minimum diameter, which interval *Weiler* (46) found to be on the average .87 sec. and *Reeves* (39, 40), 1.2 sec. *Gradle* (19, 20) concluded that there was a primary contraction of the pupil following the latent period, which lasted .4365 sec., during which the width of the pupil decreased at the rate of 5.48 mm. per sec. He also defined a secondary contraction of the pupil which lasted .3125 sec., during which time the pupil decreased at the rate of 1.34 mm. per sec. In the experimental work of *Lieben* and *Kahn* (28) the existence of two phases of the pupillary contraction was confirmed. From our own point of view it appears that this division of the contraction period into primary and secondary phases is largely arbitrary.

It is also true that the balance between the sphincter and dilator mechanisms of the iris is not only direct but consensual, *i.e.*, because of a limited decussation of the pupillary fibers in or behind the optic chiasma, impulses from one eye travel to the centers causing a reaction of both pupils simultaneously (21) (33) (36). According to *Reeves* (39, 40) when one eye was closed, the pupil subjected to a light showed the same characteristic curve of contraction as when both eyes were open but the time of contraction

was slower initially. Under a fixed intensity of light with both eyes open the pupils measured 2.7 mm., while with one eye closed the open pupil measured 3.3 mm. *Weiler* (46) stated that the consensual response was as large as the direct response. He further mentioned a summation effect brought about by stimulating one eye with a light, then transferring the stimulus to the other eye which had already shown a consensual reflex response with the result that the response of this eye was increased.

The amount of light falling upon the retina is proportional to the size of the pupil which in turn depends upon the brightness to which the eye is exposed. A pupil has a certain period for contraction which varies according to the degree of dilatation (3). In each case of contraction there is a period of latency and a time for contraction which is proportional to the amount of contraction (47). For each subject there is an individual rate of response for each intensity of light stimulation to which the eye is exposed (39).

Another aspect of pupillary activity is the rate of opening of the pupil after its subjection to a bright light. By means of flash-light photography *Reeves* (39, 40), measuring the pupil at various intervals after its exposure to a strong light, found that the pupil returned to its previously dark adapted size in five minutes. *Gradle* (19, 20) subjected the pupil to a bright light and found, by means of a motion-picture camera with a rotating sector for interrupting the illuminating beam for certain intervals of time, (1) that when the illumination was removed the pupil started to dilate at the rate of .95 mm. per sec., (2) that there was no latent period and (3) that the rate of opening was uniform with no sharp transitional points.

Measurements have been made upon the amount of light required to cause a change in the size of the pupil. *Reeves* (37) found that the diameter of the pupil was practically the same whether the illumination was 0.00015 or 0.01 millilamberts. The point of illumination beyond which the pupil ceased to contract was determined by *Reeves* (37) to be 355 millilamberts, the size of the pupil between 2.6 mm. and 2.3 mm. for 355 and 2000 millilamberts, respectively. *Schirmer* (41) has found that the varia-

tion in the size of the pupil between 100 and 1100 candleimeters was very slight.

Pupillary changes may not only be brought about reflexly but also psychically, *i.e.*, the pupil is effected by the mental or emotional states of the individual. *Weiler* (46) without statements of detail in regard to effect upon rate and other factors stated that dilatation of the pupil may be provoked by painful impressions, suddenly aroused attention and dyspnea. That this phase of pupillary reflex activity has received little exact experimentation is attested to by the statement of *Cason* (6). He said that he conducted a short experiment to determine the effect of different mental states on the size of the pupil but did not arrive at any very definite conclusions. *Lieben* and *Kahn* (28) narcotized a cat with ether and chloroform and reached the following conclusions: the emotional pupillary reaction which usually appears in an emotional state (1) disappeared under anesthesia, (2) could not be produced after decapitation, (3) disappeared after transection at the level of the soft part of the neck, (4) could be established only if the cortex was intact, and (5) presented mainly reflex inhibition of the impulses coming from the oculomotor center which maintains the tonus of the sphincter muscle.

Löwenstein (29) used such stimuli as a painful prick, a sudden fright and a slow fear. He found that fright inhibited the reaction of the pupil in the light but that a painful prick did not do so. Instead, it prolonged a subsequent dilation of the pupil after the source of light had been removed. He also found that purely psychic stimuli, coming before the light stimulus, caused the pupil to dilate and that the extent of contraction following the light stimulus was greater than the usual reaction. A delay in the reaction of the pupil of an individual affected by fright and pressure was shown in some curves but this delay did not occur with pin pricks as stimuli. When the two forms of stimuli, light and emotional, were simultaneous he found that the reaction of the pupil presented a characteristic curve with a cascade effect, *i.e.*, the pupil decreased in size in steps. With different individuals he found different types of reaction, *e.g.*, (1) a much delayed reaction and (2) a very rapid reaction. He maintained that the

individuals whose pupils exhibited the latter form of response were the most sensitive in showing a pupillary reaction which was much more extensive and a restlessness of the pupil. It should be remarked that all of *Löwenstein's* records were obtained with intermittent light flashes. Consequently, his results are not directly comparable to ours.

It is widely known that various stimuli—muscular, visceral and exteroceptive—indirectly cause a dilatation of the pupil. *Löwenstein* and *Westphal* (30) made a study of spastic muscular conditions and the accompanying pupillary changes. *Byrne* (5) found an effect on the pupil due to stimulation of the skin and viscera. *Lebensohn* (27) found that reflexes from the eye to the stomach and from the stomach to the eye are related. *Weiler* (46) considered that the pupillary reflex had an active part in connection with painful stimuli and the activity of related parts of the sympathetic nervous system. He used auditory stimuli, pin pricks and faradic current. Without measurement of the rate he found marked individual differences in reaction and that the pupillary reaction was slow and large, therefore, appearing to make very fine reactions to a great many stimuli. The result of a myriad of extraphotic influences is that the iris is probably always making fine oscillatory movements.

Besides the pupillary changes that occur reflexly and psychically, the pupil is influenced directly or indirectly by chemical stimulation. Omitting discussion of the external agents applied to the eye, such as the mydriatics and miotics, we shall consider only the investigations of the effects of alcohol. *Weiler* (46) conducted the most extensive study along this line. It should be noted, however, that his 112 alcoholic cases were of the chronic variety. Of these a small percentage showed pupillary disturbances of a rather inconsistent nature. He extended his work by selecting five average individuals and found that, after 20 c.c. of 95% grain alcohol had been ingested, there occurred no change in the size and rate of the pupillary response to light. After 40 c.c. of alcohol had been ingested he found unusual promptness in reaction and that the difference between the size of the pupil in light and dark was greater than usual. However, the latent period and contrac-

tion-time proper remained unchanged. Sollman (43) reported from a study by Hyde¹ that the latent period was increased by 5 per cent and that reflexes were depressed.

Growing out of the previous work in the field of pupillary phenomena, the present investigation undertook to study the reaction of the pupil to light while stimuli of extra-photic nature were introduced (1) before exposure to light, (2) simultaneously with exposure to light, and (3) following exposure to light at the point when the pupil had reached its minimal diameter. A period of ten minutes was allowed for dark adaptation prior to the incidence of the light stimulus. The intensity of the stimulating lights, the angle of the lights and the focal distance were controlled and kept constant. The rate of contraction was determinable and measurable for each case and the records of each subject taken under normal conditions were compared with the records obtained with the introduction of pain and emotional stimuli and after the ingestion of alcohol.

II. The mechanism of the pupillary reflex. It is known (21) (33) (36) that the iris is controlled by two reciprocating sets of muscle fibers, the circular sphincter with oculomotor innervation of the parasympathetic type, and the radial dilatator muscle fibers, innervated from the superior cervical ganglion of the sympathetic type. The sphincter is under the influence of continuous tonic constrictor impulses from the pupillary center, the tone of which is being continuously inhibited to varying degrees by afferent and emotional impulses. The diameter of the pupil of the iris is the resultant of these opposing forces.

The most active agent eliciting pupillary reflex response is light. The stimulation of light upon the retina, whether or not it causes an electrical (7) or a chemical (8) response, changes the tonicity of the iris muscles through a given pathway. According to Shastid (42) in and about the macula there are pupillomotor fibers, certain ones of which are responsive to light (photo-responsive) and others of which are responsive to darkness

¹ Hyde, S. H., Alcohol, *Kans. Univ. Sci. Bull.*, June, 1913.

(scoto-responsive). Illumination falling upon the pupillomotor area causes a change in the size of the pupil: if the illumination is increased, the pupil through these photo-responsive fibers becomes smaller; if it is decreased, the pupil through the scoto-responsive fibers becomes larger. The impulses set up run along these fibers from the macula to the optic nerve, into the nerve to the optic chiasma where they partially decussate and at length reach the pupillary contraction center in the floor of the aqueduct of Sylvius. The third nerve carries the impulse back *via* the ciliary ganglion to the sphincter muscle fibers.

The dilatation of the pupil is not entirely due to the relaxation of the sphincter pupillae muscle but is partly due to the contraction of the dilatator pupillae muscles which are kept in a state of tonic contraction by impulses emanating from a nerve center in the medulla oblongata. The axons which arise in this center pass down the cord, emerge through the first thoracic nerve and then ascend to the superior cervical ganglion. From these cells new axons of the sympathetic system arise which pass to the long ciliary nerve and subsequently to the dilatator muscles of the iris.

The variations in the size of the pupil, although largely a reflex response under the control of the oculomotor nerve, are nevertheless partly due to the active coöperation of the dilatator nerves and their related muscles. The size of the pupil, necessary from moment to moment for the admission of just that amount of light essential to the formation and perception of a distinct image, is the result of two nicely adjusted and delicately balanced forces. When one set of muscles, due to stimulation, constricts, the other set relaxes, and *vice versa*.

There are many forms of stimulation, however, which directly and indirectly, by virtue of the chain of connections with the sympathetic nervous system, will cause a disruption of this equilibrium. The present study investigated certain various interrelationships between the two balancing forces in pupillary reflex activity by introducing stimuli which would possibly alter the normal pupillary reflex to light.

III. Apparatus. The apparatus consisted of a moving-picture

camera, stimulus lights, synchronous motor to operate the camera, and a device for holding the head rigidly in position while photographing the eye (Fig. 1).

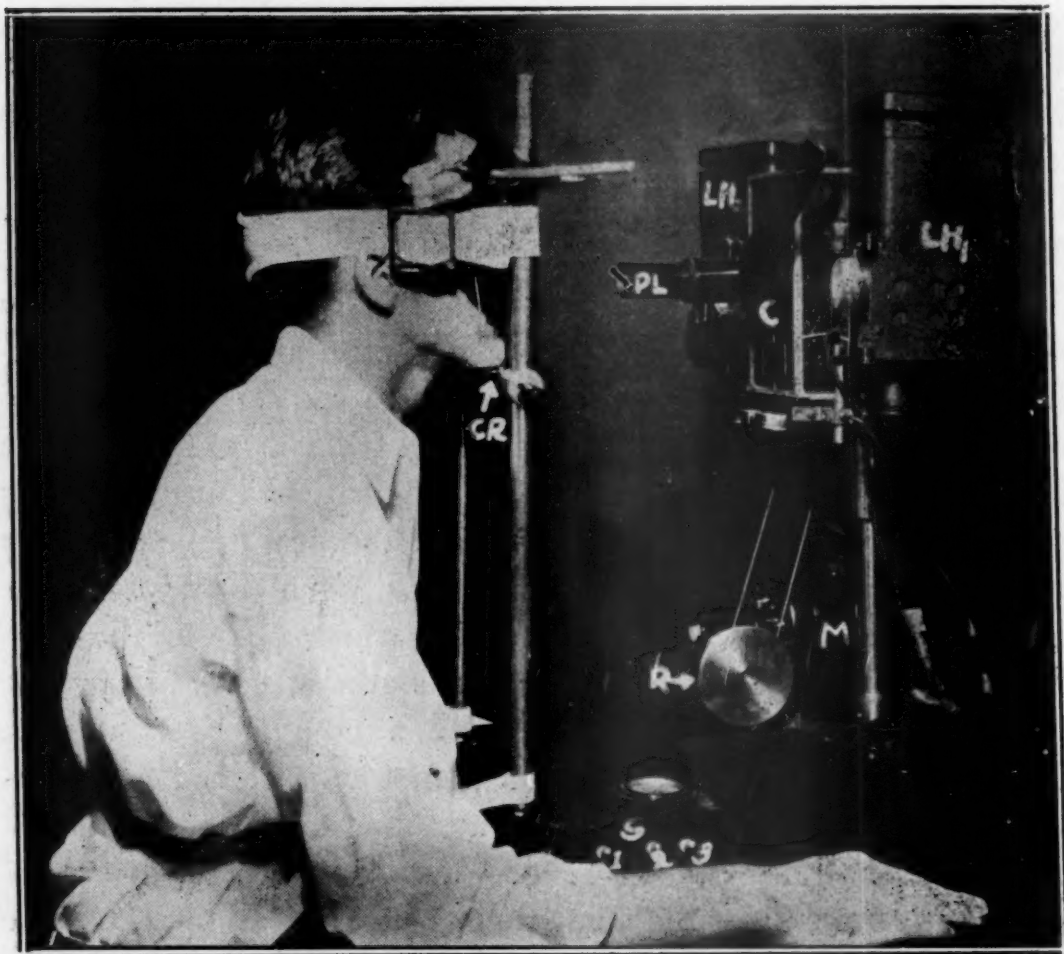


FIG. 1. Apparatus for photographing the pupil. CR=chin rest. C=camera. PL=projected lens barrel. LH₁ and LH₂=lamp-houses enclosing stimulus and photographic lights. M=motor. R=reducing gear. S=switchboard, 1=motor, 2=lights, 3=shutter-drops. Subject in position with head fixed firmly and waist strap adjusted.

The motor was driven by a sixty cycle alternating current. It revolved 1800 times per sec. and was connected to the camera through a 10 to 1 reducing gear by a spring-wire pulley belt. This speed, three revolutions per sec., exposed 24 sections of film per sec.

The camera was an Eastman Ciné Kodak Model A with a 68 mm. anastigmatic f. 4.5 lens. In the lens barrel was a double prism which transmitted 90 per cent of the light to the film and reflected 10 per cent for focusing. The lens was extended out

beyond the usual mounting because of the necessity for close working distance—approximately 10 mm. from the film and 10 mm. from the eye of the subject. There was an 180 degree shutter which gave 1/48th of a sec. exposure at 24 revolutions per sec. The aperture was adjustable. The whole camera which was mounted on a platform one foot above the base could be rotated, raised or lowered and adjusted for proper focal distances.

The stimulus lights consisted of two high pressure 50 v. 200 w. concentrated filament lamps. At the same level with the lens, 6 mm. on either side of the camera, each light was situated in a lamp-house with a "bull's eye" condenser and concave mirror and reflector for doubling the light. The lamp-houses could be adjusted for any angle and after focus could be set to move when the camera was moved. The stimulus lights were 35 mm. from the eye. There was a shutter over each lamp which was released by a solenoid actuated by a 4 v. dry battery. The lights were adjusted to focus on one spot so that forward or backward adjustment could bring the focal point upon the pupil of a subject's eye. The intensity at this point was measured by a Betz photometer and the combined power of the two lights was found to be 960 foot-candles.

The above mentioned parts were all mounted on a steel base, 14 in. x 18 in. x 3 in. At the front edge were two 23 in. steel rods, vertically mounted, $8\frac{3}{8}$ in. apart. There was an adjustable steel cross-bar carrying a chin-rest. At the top of the vertical rods were two adjustable padded pieces of metal which conformed to the shape of the front and sides of the head. From the vertical bars was a wide band of canvas which was strapped around the head and another canvas strap to fit around the waist of the subject to help eliminate strain. The apparatus carried a switch-board which controlled lights, motor and shutter-drops. Sixteen millimeter Ciné Kodak supersensitive panchromatic safety film in 100 foot rolls was used.

IV. Procedure. All photographing was done in a small dark room. Each subject was placed in a comfortable sitting position with chin resting upon the chin-rest. Stimulus lights were focused on the pupil. The subject's head was then fastened securely and

the waist-strap adjusted. The camera was set for the proper focus. Following this the lights were switched on and off several times so that each subject would become accommodated to the glare. This was done for the purpose of cautioning the subject about blinking and winking when being photographed. The subjects were asked to become as relaxed as possible, to keep their eyes open during the period for dark adaptation, to fixate on a point on the camera box at 28 mm. distance, and not to look at either light or into the projection lens.

All lights in the room were then turned off and ten minutes were allowed for dark adaptation. At the conclusion of this time the motor was started and allowed to gain maximal and constant speed. The stimulus lights were turned on at this time and remained on from 5 to 10 sec. During the time the lights were on the experimenter observed the pupil of the subject through a right-angle lens to note if the eye was in focus. The right eye was always photographed and the left eye was always open. The light intensity never varied from subject to subject or from picture to picture on the same subject. The distance of the lens and camera from the eye was kept constant from one sitting to the next with all subjects. The angle of light remained constant and the speed of the film never varied. If a subject could not fixate, he was requested to look straight ahead when the lights were flashed on. This procedure was repeated in all of his subsequent photography.

The subjects selected for the purpose of studying the possible extent of day-to-day fluctuation of the pupillary rate of contraction under the same conditions were run twice a day for three or four days. Those persons subjected to pain and emotional stimulation were studied under normal conditions two or three times prior to the time when stimuli such as, gun shot, painful pinprick, pinch, electrical shock of 25 v. and the presentation of a white rat were introduced. These stimuli were introduced in the following manner for different subjects: (1) immediately preceding exposure to light, (2) simultaneously with exposure to light, or (3) following exposure to light when the pupil had reached its maximum contraction. Two or three subjects were forewarned of the appearance of a stimulus.

Those subjects used in the study concerned with the alcoholic effect furnished a series of records before the ingestion of any alcohol, under normal conditions, and after each ingestion of 20 c.c. of alcohol. Dark adaptation of ten minutes was allowed after each ingestion. The subjects were given 20 c.c. of 95 per cent alcohol every fifteen minutes in 200 c.c. of "near beer" as the vehicle. No subject ingested less than 100 c.c. nor more than 120 c.c. of alcohol. Between successive pictures all subjects were allowed five minutes' rest in addition to the period for dark adaptation. If a subject blinked or moved out of focus another picture was taken. Each picture was taken with an exposure of film from 5 to 10 sec.

Each frame of film was displayed by a "Kodatoy" projector on a screen and measured in centimeters. The projection distance enlarged the pupil exactly 10 times. No attempt was made to measure the actual diameter of the pupil. The apparent diameter of the pupil as it appeared on the film for each subject was uniform and the same scale was employed in all measurements.

V. Subjects. Because it was found that brown irises would not show a clear definition of the pupil on the film all cases selected for photographing were blue-eyed. They ranged in age from 18 to 32 years; there were 10 females and 9 males. The subjects are to be grouped as follows:

(1) Four normal adult females who were run twice a day for three or four days to determine possible variability in pupillary reflex activity.

(2) Eight normal adults, 6 males and 2 females, who were subjected to emotional stimuli before or simultaneously with exposure to light to determine the effects of this form of stimulation upon the pupillary reflex activity.

(3) Five normal adults, 4 males and 1 females, who were subjected to pain stimuli before or simultaneously with exposure to light to determine the effects of this form of stimulation upon the pupillary reflex activity.

(4) Two normal adults, 1 male and 1 female, who were subjected to pain and emotional stimuli after exposure to light when the pupil had reached its minimal diameter to determine the effects upon the pupillary reflex activity.

(5) Three normal adult male subjects who ingested various amounts of alcohol to determine the subsequent pupillary reflex activity. These may be considered briefly individually:

Subject HOJ. Age 24 yrs., weight 160 lbs.; moderately intoxicated but once approximately two years before the experiment; health excellent.

Subject RP. Age 24 yrs., weight 150 lbs; drank moderately from once to three times a month for the past three years; prior to the experiment he had not drunk for six weeks; health excellent.

Subject CCJ. Age 28 yrs., weight 195 lbs.; drank moderately for the past two years and irregularly once every three months; prior to the experiment had not drunk for three months; health excellent.

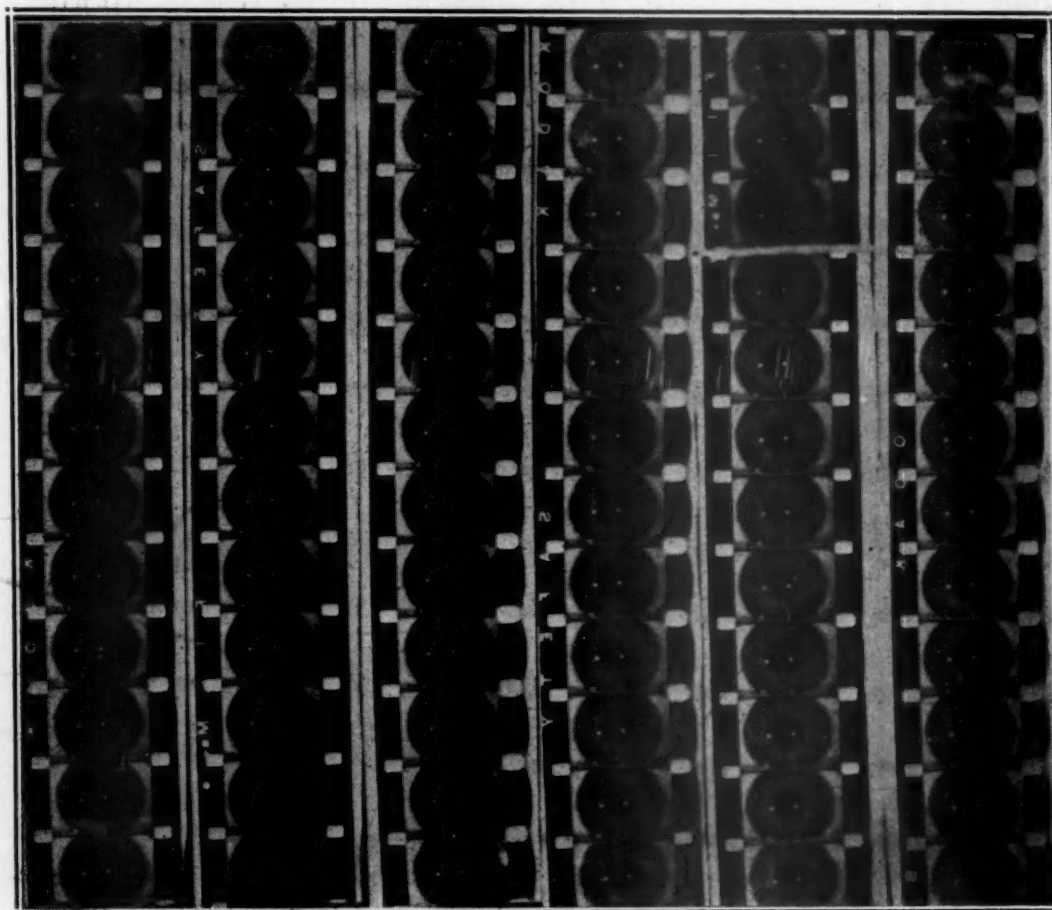


FIG. 2. Photographic record of the right eye of subject AB following a ten minute period for dark adaptation. Stimulus was 960 ft. candles of light. The beginning of the record is at the upper left hand corner.

*VI. Results.*² Fig. 2 is a sample of the records obtained in this study. Following the period for dark adaptation at the

² Complete tables containing measurements of the pupil on which statements in the study are based are to be found in the author's doctorate dissertation (1932) on "The effect of pain and emotional stimuli and alcohol upon pupillary reflex activity," on file in the Library, Univ. of Iowa, Iowa City, Iowa.

moment the stimulus light was applied the pupil was large. It remained large for a short interval of time (the latent period) after which it rapidly decreased in size until it reached its minimal diameter (the contraction period). Each frame of film represents 1/24th of a sec.

(1). *Variability in pupillary reflex activity from day to day.* From Figs. 3, 4, 5 and 6 it is apparent that there was marked

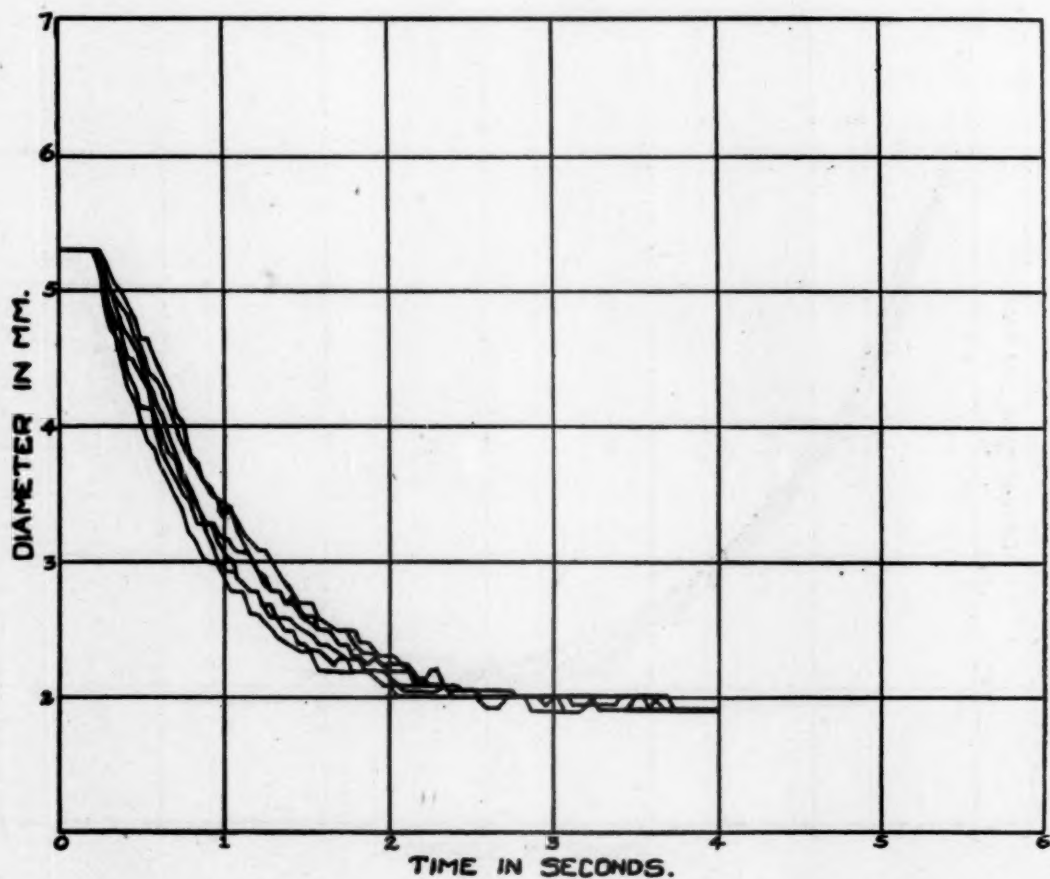


FIG. 3. Graph of 6 records of the pupillary reflex contraction on different days for subject AB.

consistency in the pupillary reaction from day to day under the same conditions for normal subjects. Subject AB showed the greatest and subject PK the least amount of variation. On all records the period of time giving the major portion of the contraction (approximately 1.5 sec. following the latent period) exhibited the greatest amount of variation. The records of AB showed that the diameter following dark adaptation was the same on each, 5.3 mm.; that the latent period was .20 sec. on 5 records

and .25 sec. on one; and that the pupil reached its minimal diameter on 4 records in 3.5 sec. and on 2 records in 3.0 sec. Six records of subject EI revealed that the diameter following dark adaptation was the same (6.0 mm.) on 3 occasions, and the same (5.8 mm.) for 3 other records; that the latent period of 5 records was .16 sec. and for one record was .12 sec.; that the minimal diameter was reached at the end of 4.0 sec. on all 6 records. Six



FIG. 4. Graph of 6 records of the pupillary reflex contraction on different days for subject EI.

records of subject HJ showed no variation from record to record for the diameter of the dark adapted pupil, 5.2 mm., the latent period, .20 sec., and the minimal diameter at the end of 3.75 sec. The 6 records of subject PK showed no variation from record to record for the diameter of the dark adapted pupil, 5.9 mm., the latent period, .20 sec., and the minimal diameter at the end of 3.5 sec.

Reeves (39, 40) stated that the size of the pupil under normal

conditions varied only slightly from day to day. The .25 mm. average deviation found in the present study with the subject AB who gave the largest deviation is but 5.8 per cent of the average diameter of the pupil at the end of .5 sec. This amount of fluctuation is strikingly small in comparison with the changes which are to be reported later. It is possible that had more records been obtained the deviation would have been even less. Certain fac-

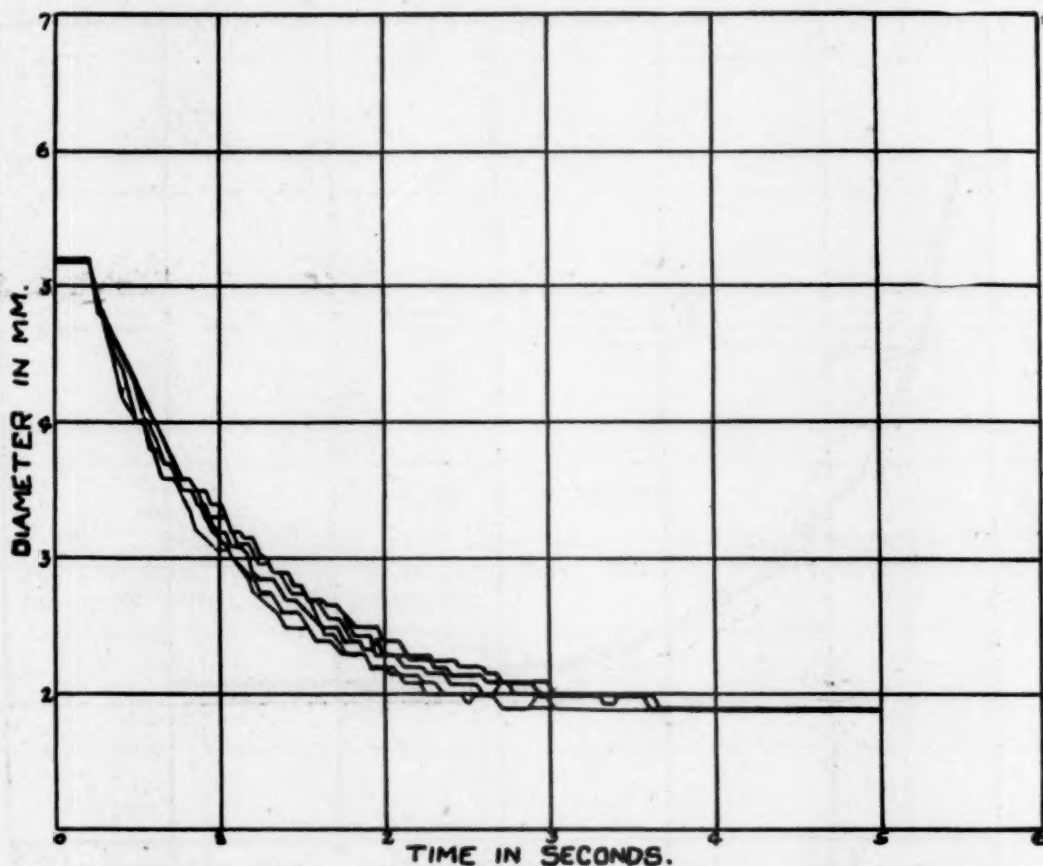


FIG. 5. Graph of 6 records of the pupillary reflex contraction on different days for subject HJ.

tors which might have influenced the results to increase the apparent fluctuation were errors in measurement and the possibility that a subject did not focus on the proper focal point throughout a record and on the same focal point from sitting to sitting.

(2). *The effects of emotional stimuli upon pupillary reflex activity.* The results of those persons subjected to emotional stimuli revealed several important facts. The latent period for

one subject remained the same while for seven subjects it increased by as much as .05 sec. to .17 sec. for the emotional pupillary reactions as compared with the normal. The rate of contraction remained the same for one subject but for seven subjects it took longer for the pupil to reach its minimal diameter by from .5 sec. to more than 5.0 sec. The diameter of the pupil, following the period for dark adaptation at the instant the light stimulus was

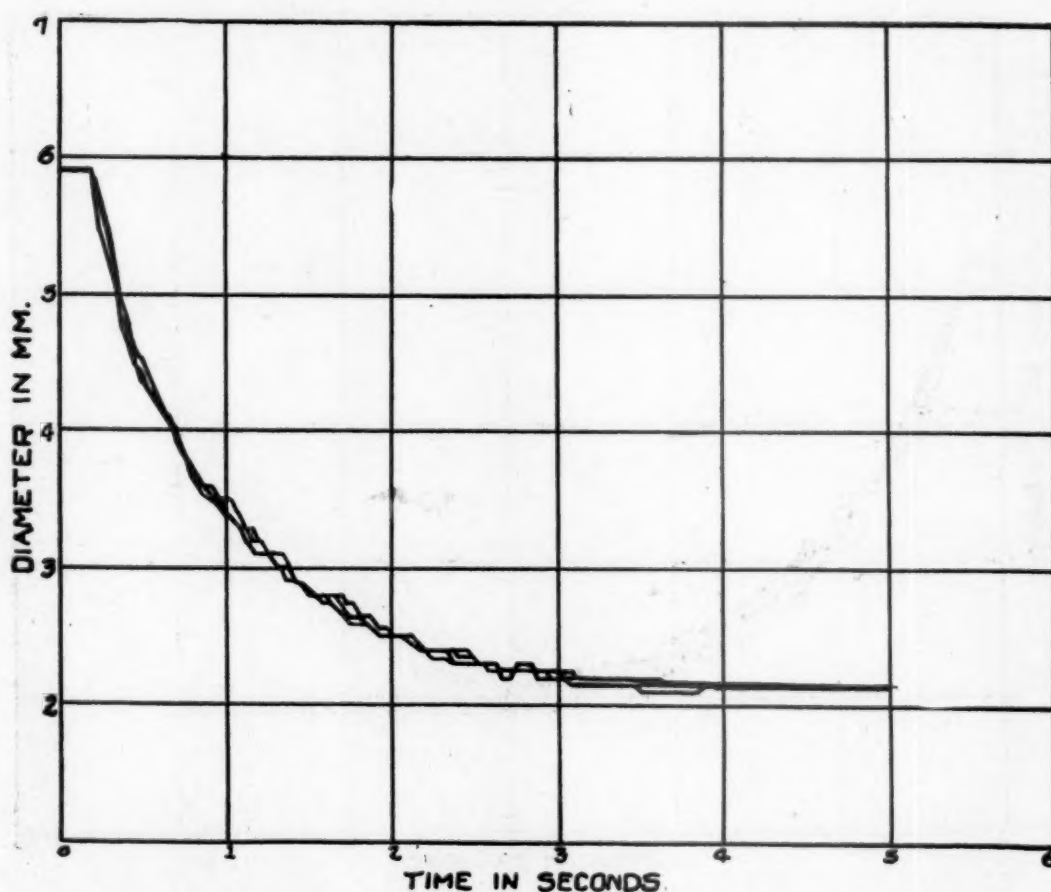


FIG. 6. Graph of 6 records of the pupillary reflex contraction on different days for subject PK.

admitted, remained the same for four subjects and was enlarged by from .2 mm. to as much as 1.2 mm. over its normal size for four subjects.

Fig. 7 illustrates the effect of a gun shot coming at the same instant as the light stimulus. The diameter of the pupil increased 1.2 mm., the latent period increased from .20 to .25 sec., and it took longer for the pupil to reach its minimal diameter. Figs. 8,

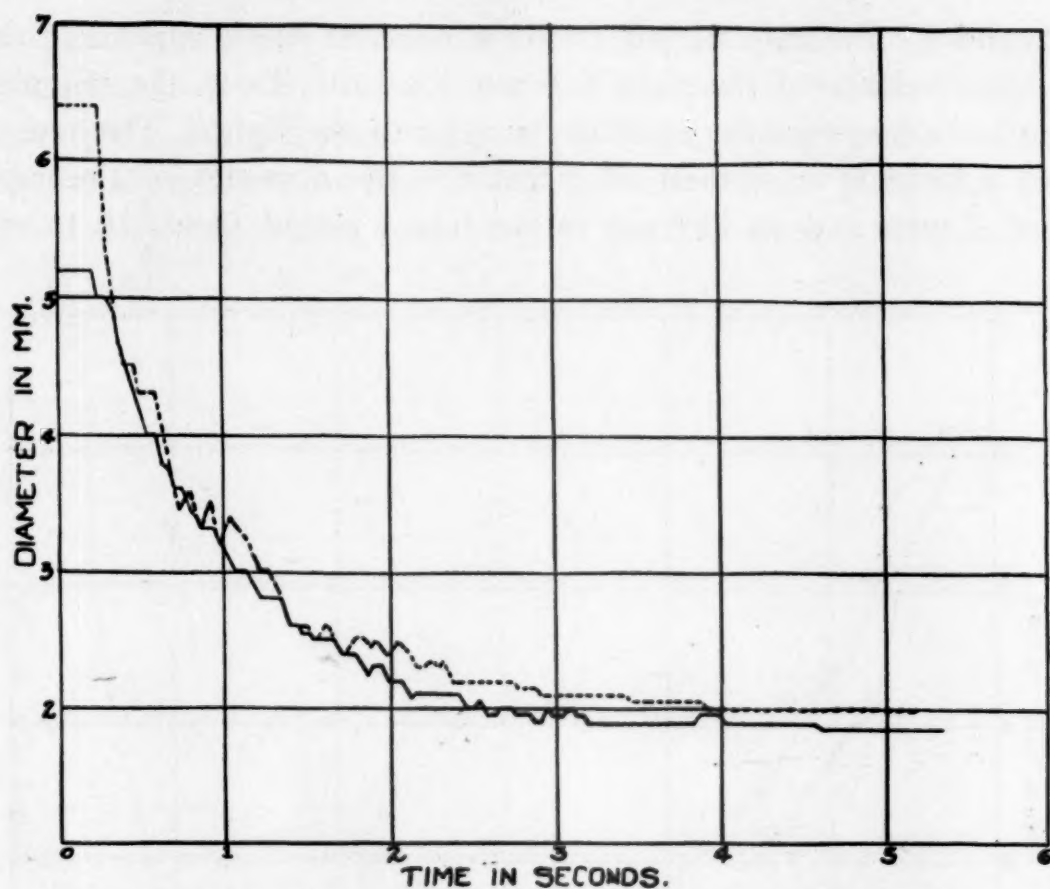


FIG. 7. Subject MLE. Solid line—the average normal contraction curve and the dotted line—the contraction curve following a gun-shot given simultaneously with the light stimulus.

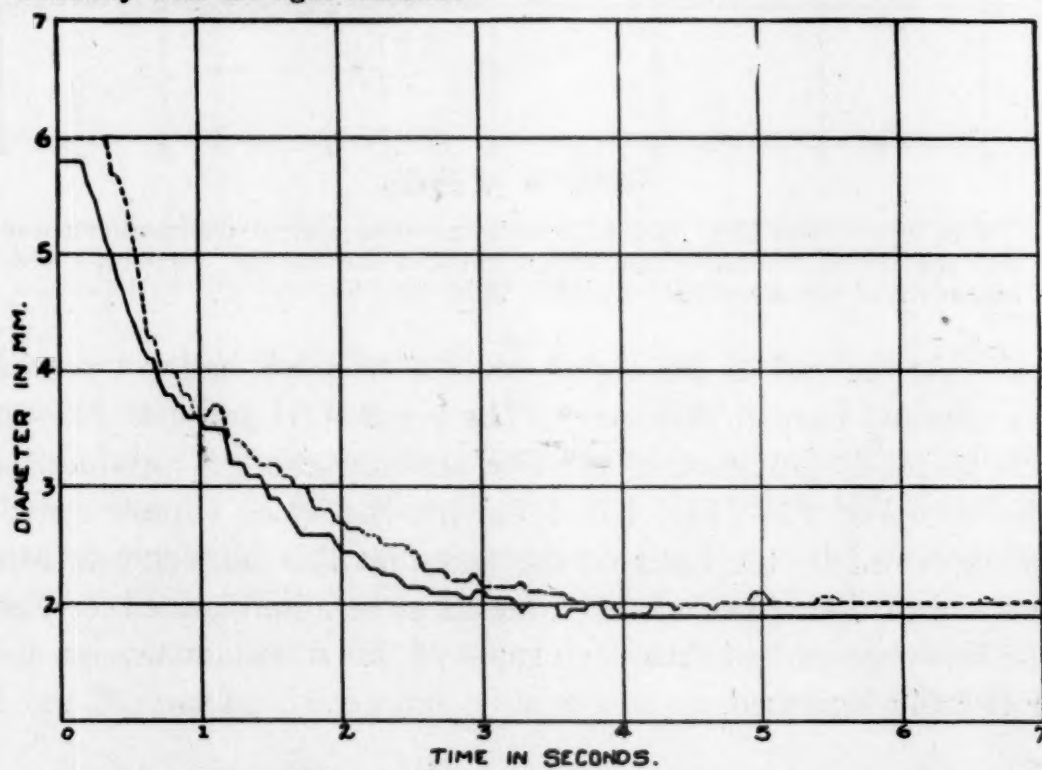


FIG. 8. Subject MW. Solid line—the average normal contraction curve and the dotted line—the contraction curve following an electrical shock administered simultaneously with the light stimulus.

9 and 10 illustrate the effects of an electric shock applied to the radial surface of the right forearm near the elbow, the stimulus in each case coming simultaneously with the light. The record of subject MW showed an increase in the diameter of the pupil by .2 mm. and an increase in the latent period from .16 to .33

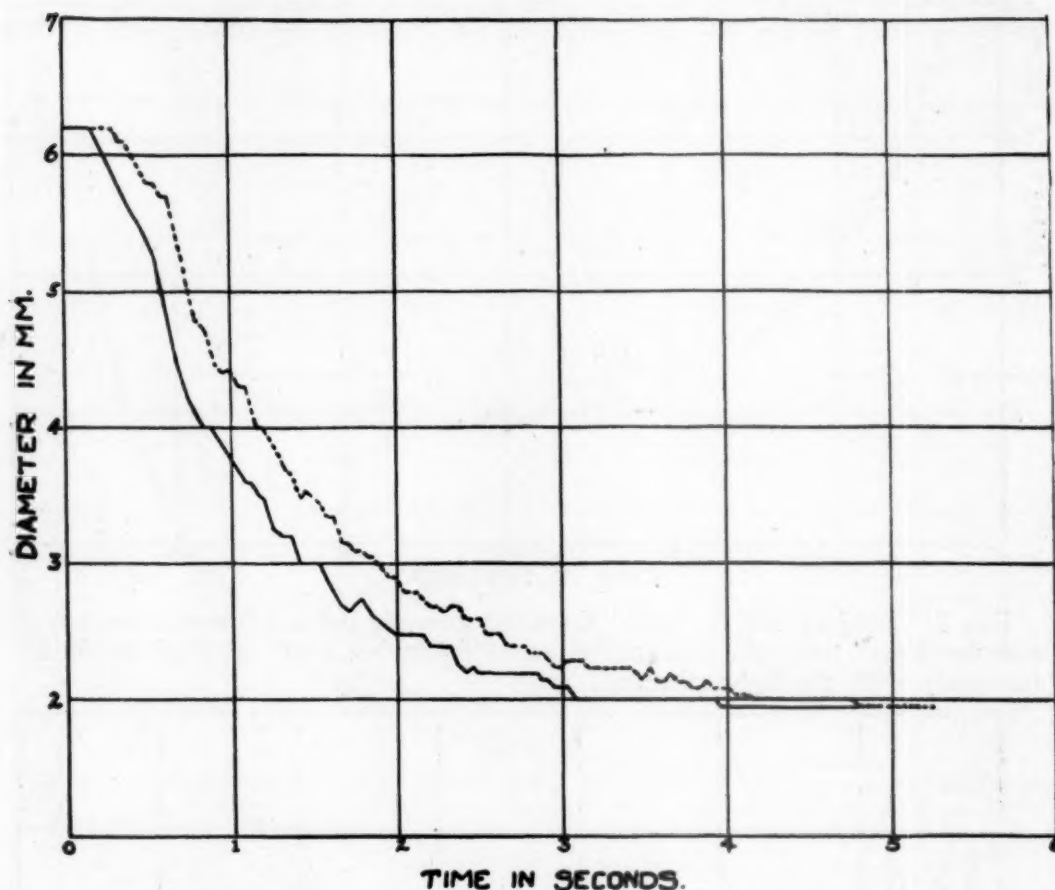


FIG. 9. Subject HS. Solid line—the average normal contraction curve and the dotted line—the contraction curve following an electrical shock administered simultaneously with the light stimulus.

sec. At the end of the eighth second the pupil had not reached its minimal normal diameter. The records of subjects HS and PN showed similar results. The striking changes produced in the record of PN (Fig. 10) following the shock stimulus might be explained on the basis of the fact that this subject was forewarned of the nature of the stimulus to be administered. When the information had thus been supplied, his muscular tension was noticeably increased.

Fig. 11 illustrates the changes produced following the presentation of a white rat as the stimulus. Simultaneously with the light stimulus a live rat was placed in the hand of subject PK. The record showed no increase in the diameter of the pupil, but the latent period increased from .20 sec. to .29 sec. and the minimal

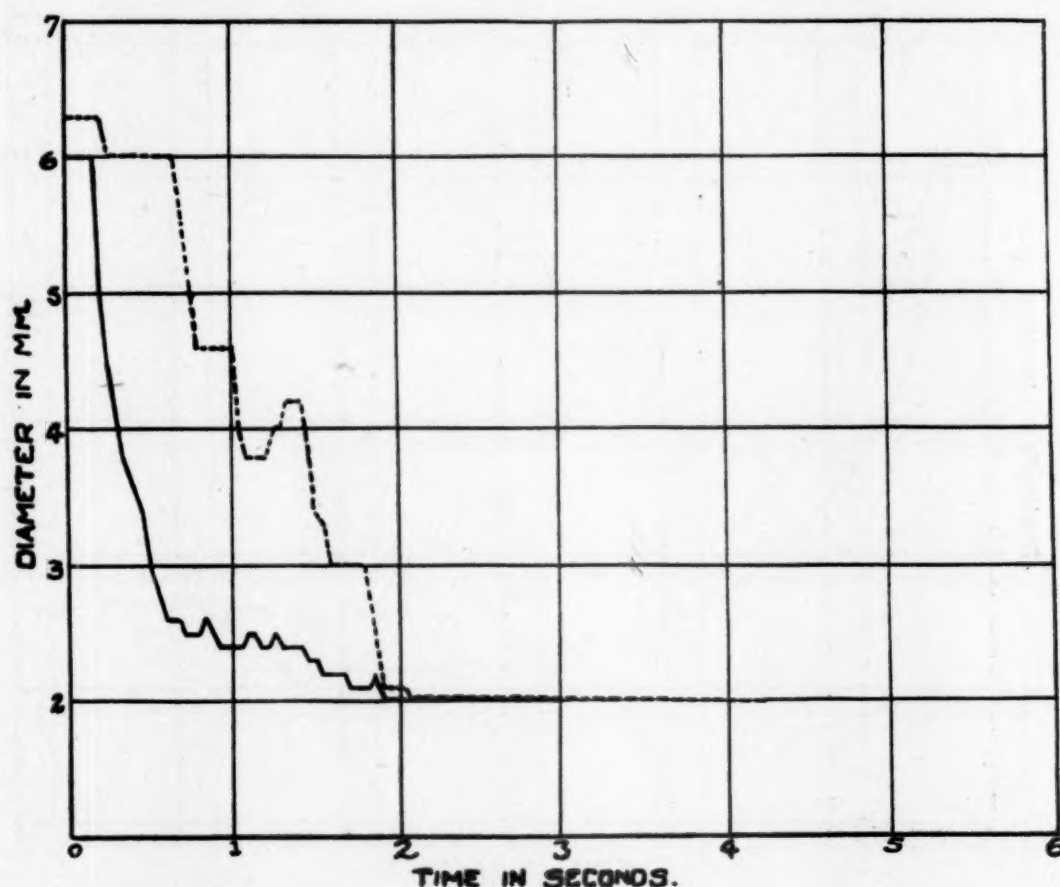


FIG. 10. Subject PN. Solid line—the average normal contraction curve and the dotted line—the contraction curve following an electrical shock administered simultaneously with the light stimulus.

diameter reached at the end of the eighth second was .5 mm. greater than the normal.

(3). *The effects of pain stimuli upon pupillary reflex activity.* The effects of painful stimuli upon the size of the pupil and the rate of pupillary contraction were very slight and the results were inconsistent. The latent period remained the same for three subjects, increased from .16 sec. to .20 sec. for one, and decreased from .20 sec. to .16 for two. The rate of contraction remained

the same for five subjects but it required .5 sec. longer for the size of the pupil to reach the minimal normal diameter for one. The diameter following dark adaptation remained the same for four subjects, increased from 5.2 mm. to 5.8 mm. for one and decreased from 5.4 mm. to 5.2 mm. for another. There was a tendency

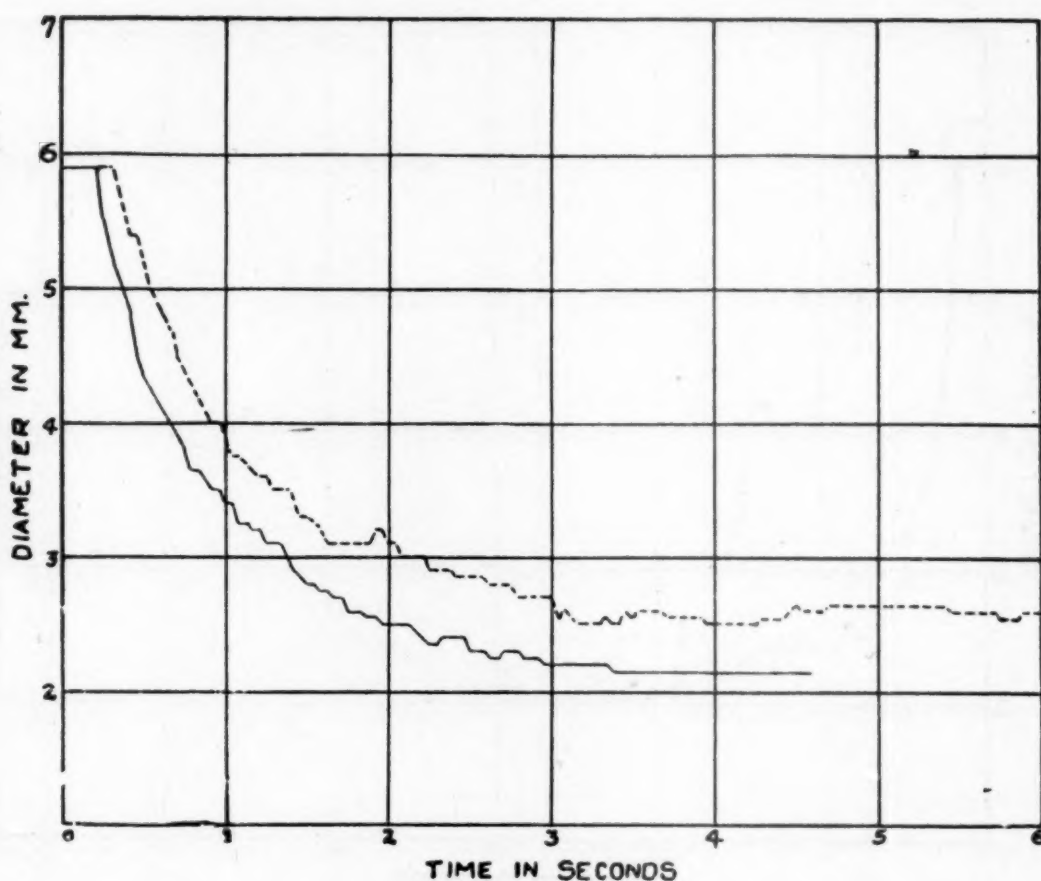


FIG. 11. Subject PK. Solid line—the average normal contraction curve and the dotted line—the contraction curve following the presentation of a white rat simultaneously with the light stimulus.

for these subjects, however, to show a more rapid initial contraction.

Figs. 12 and 13 present the records of two persons subjected to painful stimuli. HCJ was pricked with a pin on the neck and subject MS on the right forearm simultaneously with the presentation of the light stimulus. Both of these subjects showed a more rapid initial contraction following the painful stimuli. Subjects DD, MLE and MW for whom no graphs are offered gave

no significant and consistent pupillary changes following the painful stimuli.

(4). *The effects of stimuli following light stimulus and minimal contraction upon pupillary reflex activity.* Subjects RJ and MW were given an electrical shock and a painful pin prick, respec-

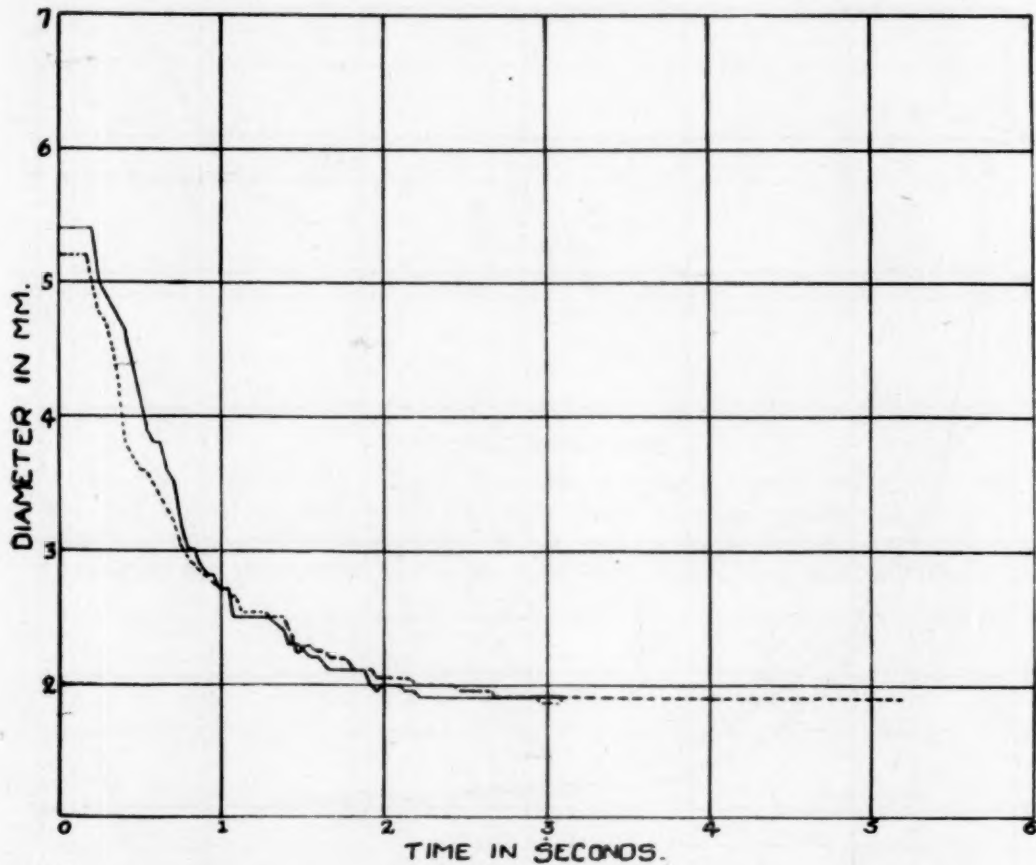


FIG. 12. Subject HCJ. Solid line—the average normal contraction curve and the dotted line—the contraction curve following a painful pin prick on the neck.

tively, after their pupils had reached the minimal diameters. Figs. 14 and 15 show that immediately following the electrical shock and the pin prick the pupil fluctuated in size over a small range. There was no large dilatation but an indication of unrest which was characterized by oscillations in the diameter of the pupils.

(5). *The effects of alcohol upon the pupillary reflex activity.* The results obtained from this phase of the study are incon-

sistent. Subjects RP and CCJ showed practically no changes in the size of the pupil, the latent period, and the rate of contraction after 20 c.c. of alcohol had been ingested. HOJ, however, indicated a more rapid contraction, showed an increased diameter of the pupil following the period for dark adaptation and a smaller

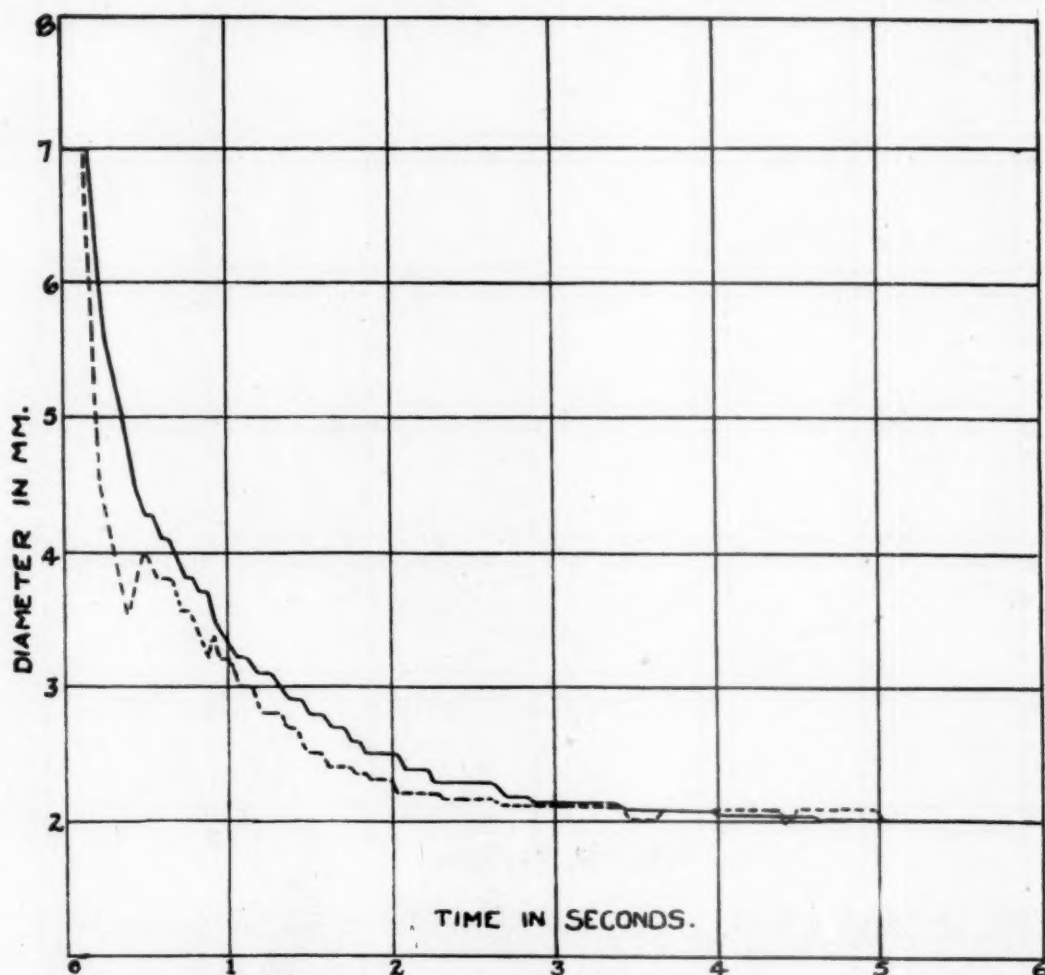


FIG. 13. Subject MS. Solid line—the average normal contraction curve and the dotted line—the contraction curve following a painful pin prick on the right forearm simultaneously with the light stimulus.

minimal diameter. After 40 c.c. of alcohol had been ingested RP and CCJ both showed an unusual promptness of reaction, a smaller initial diameter of the pupil following dark adaptation and an inability of the pupil to reach a normal minimal diameter after 6.0 sec. Following the ingestion of more alcohol HOJ showed a return to the normal in latent period and rate of contraction. He showed practically no changes after 100 c.c. of

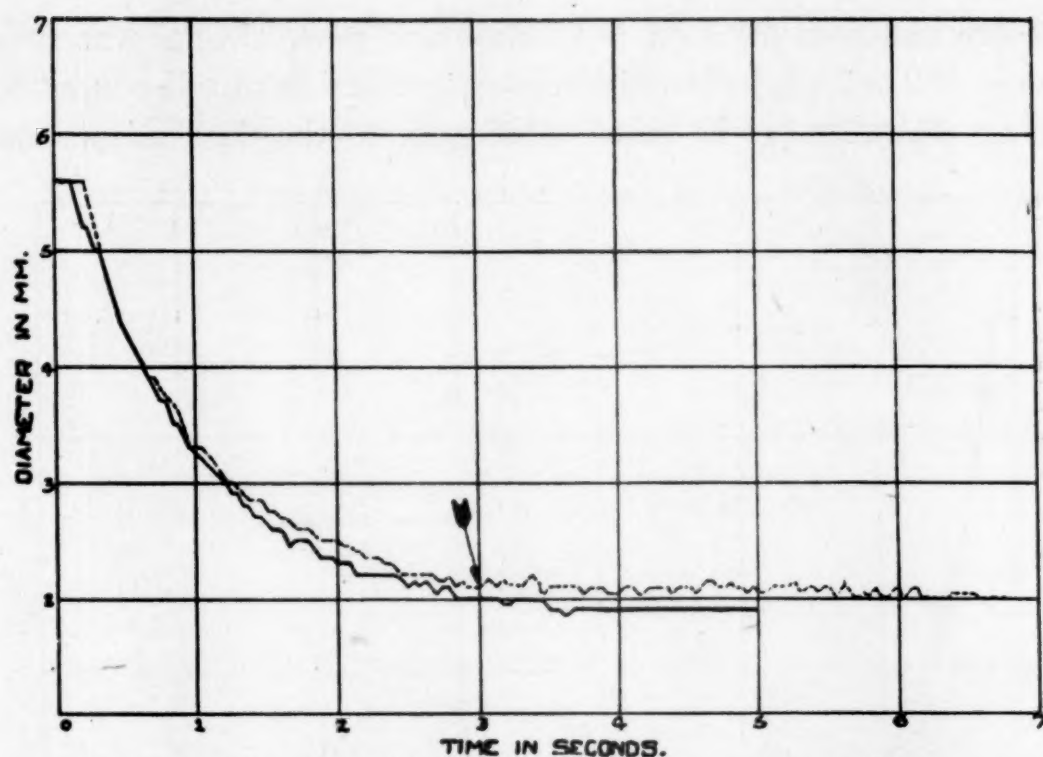


FIG. 14. Subject RJ. Solid line—the average normal contraction curve and the dotted line—the contraction curve for the period in which the stimulus was applied after the pupil had reached its minimal diameter (indicated by the arrow when the electrical shock was administered).

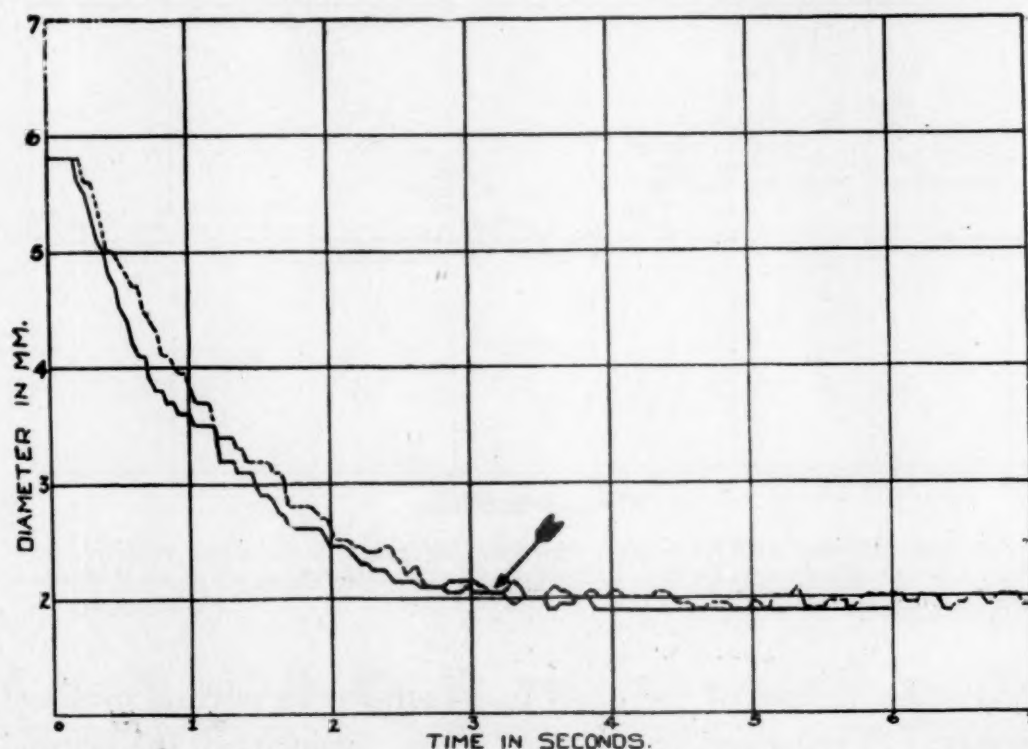


FIG. 15. Subject MW. Solid line—the average normal contraction curve and the dotted line—the contraction curve for the period in which the stimulus was applied after the pupil had reached its minimal diameter (indicated by the arrow when the painful pin prick was applied).

alcohol had been ingested. As more and more alcohol was consumed RP and CCJ showed a slower contraction time, an increase in the diameter of the pupil subsequent to the dark adaptation

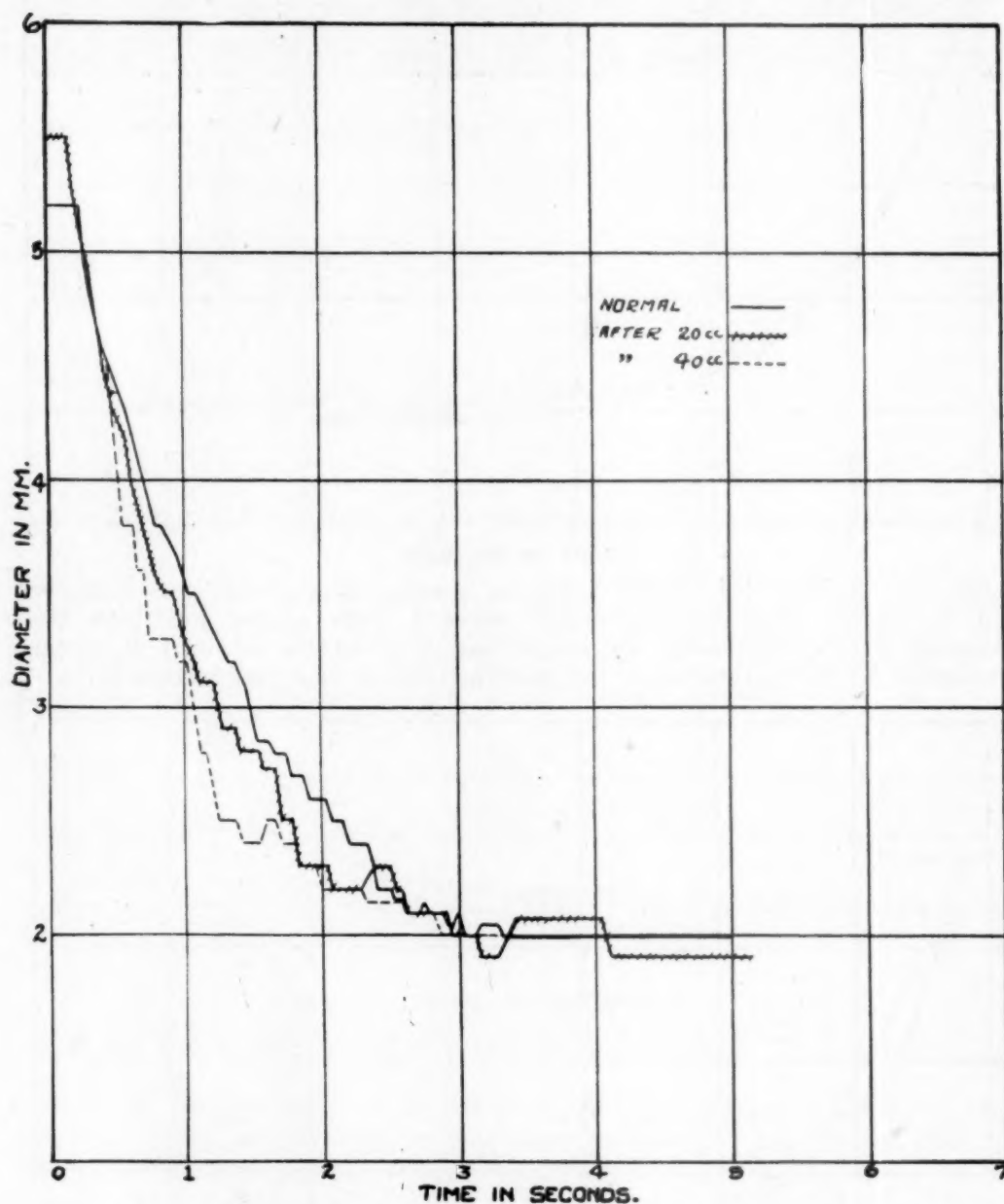


FIG. 16. Subject HOJ. Graph representing records obtained at different stages of alcoholic intoxication as compared with the average normal curve of contraction.

period and a failure of the pupil to return to the normal minimal diameter. It remained from .4 to .5 mm. larger than the normal minimal diameter. Figs. 16, 17, 18 illustrate the findings on

the three alcohol cases. All records were not graphed because some did not show significant deviations from the normal.

(6). *Pupillary reflex changes in terms of percentages.* Tables

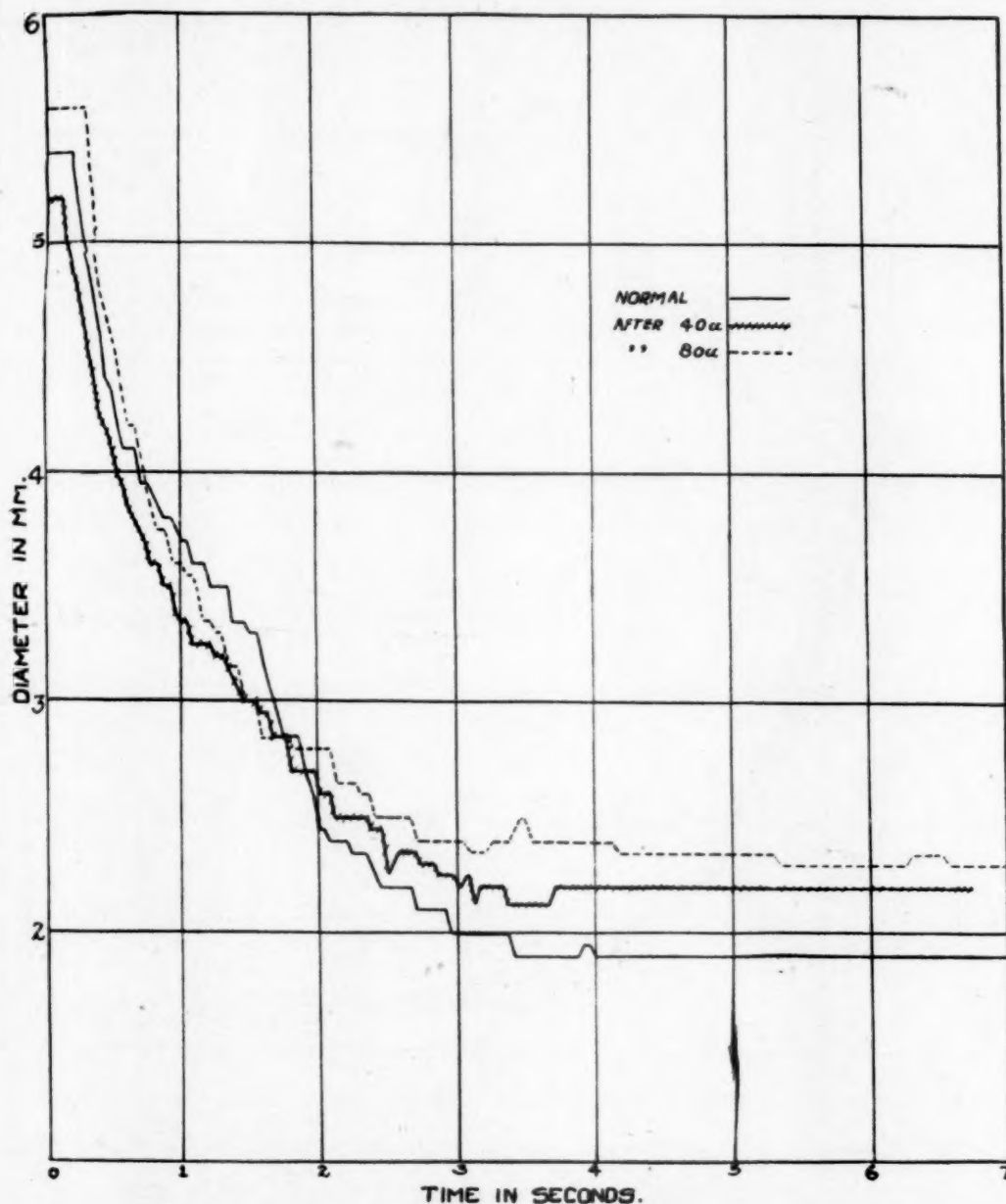


FIG. 17. Subject RP. Graph representing records obtained at different stages of alcoholic intoxication as compared with the average normal curve of contraction.

I, II, III and IV give the percentage variations of records obtained under various experimental conditions as compared with those obtained under normal conditions.

In Figs. 3 to 18, inclusive, pupillary contraction fluctuations and changes have been graphed in terms of absolute amounts in

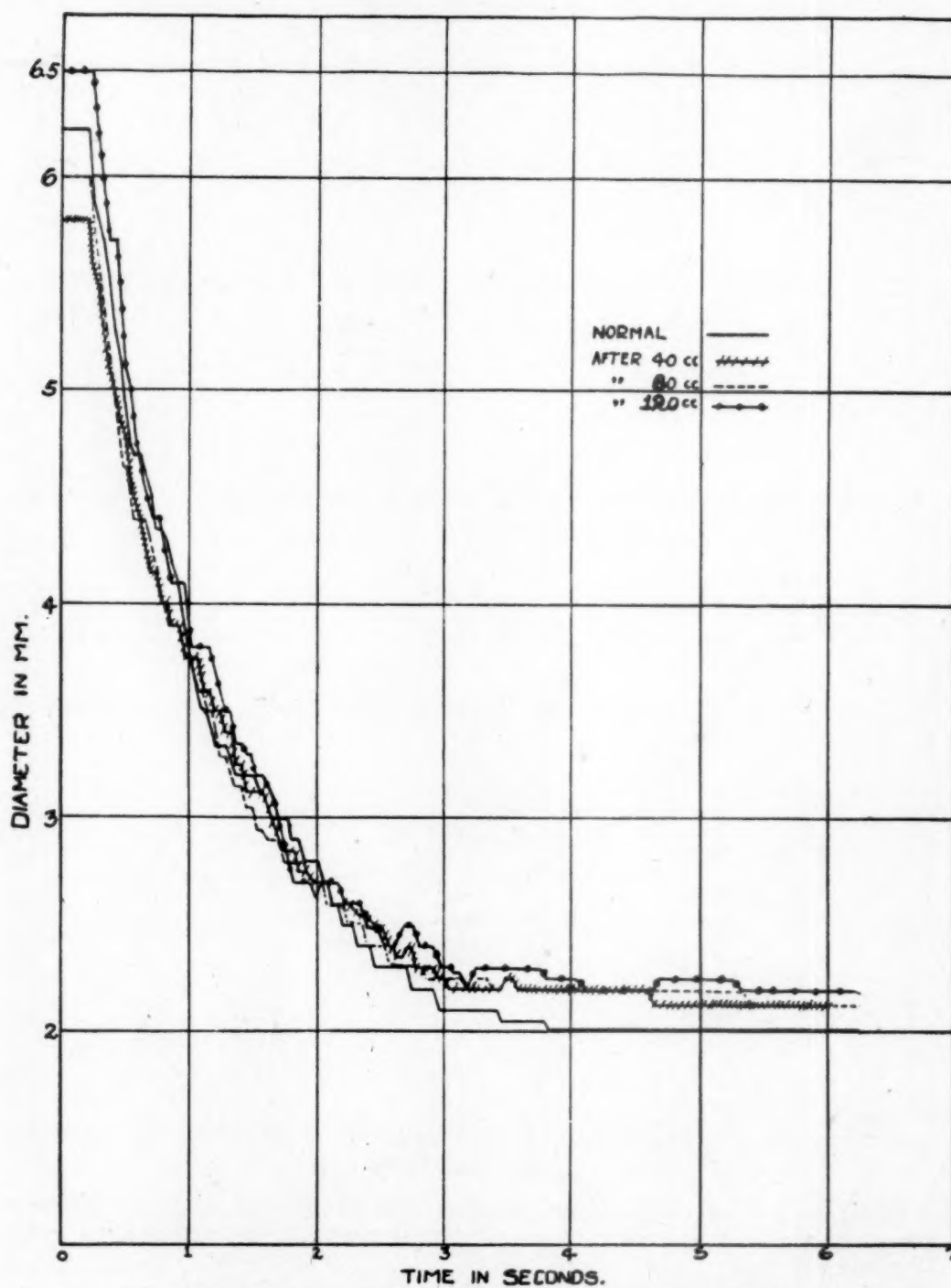


FIG. 18. Subject CCJ. Graph representing records obtained at different stages of alcoholic intoxication as compared with the average normal curve of contraction.

mm. In the tables these changes are presented in terms of percentage deviations from the averages of the diameter readings of

normal records at the different time intervals. The average percentages presented in Table I are to be considered the ones with

TABLE I. *Average deviations in terms of percentage of day to day records taken of subjects under normal conditions*

Interval	AB	EI	HJ	PK	Average
0.5 sec.	5.8	4.2	2.4	0.6	3.2
1.0 "	5.4	2.4	2.5	0.0	2.6
1.5 "	5.6	2.8	3.0	0.7	3.0
2.0 "	4.1	4.0	2.6	1.2	3.0
2.5 "	2.4	3.5	3.8	1.7	2.9
3.0 "	1.5	3.8	2.5	0.0	1.9
3.5 "	0.0	1.5	2.0	0.9	1.1
4.0 "	0.0	0.0	0.0	0.0	0.0
5.0 "	0.0	0.0	0.0	0.0	0.0

which all percentages of variation in subsequent tables may be compared. For example, for the four subjects (Table I) the average percentage fluctuation from day to day for the 0.5 sec. interval for the readings obtained under normal conditions was 3.2 while the percentage of change for subject PK (Table II) for the 0.5 sec. interval was 16.8.

TABLE II. *Percentage variations from the normal produced by emotional stimuli*

Interval	MLE	GK	EH	PMW	PN	HS	MW	PK
0.5 sec.	2.0	19.0	9.0	5.4	100.0	7.4	20.0	16.8
1.0 "	1.4	26.0	6.0	0.0	91.0	21.6	0.0	14.7
1.5 "	1.9	11.0	3.0	0.0	47.0	16.6	10.0	15.8
2.0 "	9.0	8.0	0.0	1.0	5.0	16.0	8.0	26.5
2.5 "	10.0	13.0	4.0	0.0	0.0	18.0	9.0	24.8
3.0 "	7.0	16.0	0.5	0.0	0.0	9.0	0.0	15.9
3.5 "	8.0	5.0	7.8	0.0	0.0	10.0	0.0	23.8
4.0 "	5.0	5.0	8.0	0.0	0.0	5.0	0.0	16.4
5.0 "	8.0	5.0	0.0	5.0	0.0	23.2

It may be seen that under emotional stimuli certain subjects presented striking changes as compared with the changes incident to the normal day to day fluctuations. Only one subject (PMW) in the group subjected to emotional stimuli showed no striking changes while the other seven presented percentage deviations up to 100 per cent for most of the intervals up to and including the fifth second. Only one subject (Table III) out of the six subjects in the group confronted with painful stimuli presented anything like outstanding percentage deviations from the normal conditions.

TABLE III. *Percentage variations from the normal produced by pain stimuli*

Interval	DD	DD	MLE	HCJ	MS	MW
0.5 sec.	2.0	5.0	2.0	14.0	11.0	4.5
1.0 "	6.0	6.0	1.0	0.0	0.0	0.0
1.5 "	7.0	11.0	2.0	2.0	10.0	3.0
2.0 "	4.0	0.0	0.0	2.0	12.0	2.0
2.5 "	2.0	2.0	0.0	2.0	6.0	0.0
3.0 "	2.0	0.0	0.0	0.0	2.0	0.0
3.5 "	2.0	0.0	0.0	0.0	0.0	0.0
4.0 "	0.0	0.0	0.0	0.0	0.0	0.0
5.0 "	0.0	0.0	0.0	0.0	0.0	0.0

The records of the subjects (Table IV) following the ingestion of various amounts of alcohol revealed percentage variations greater than the normal in two out of three cases. The records of HOJ after each 20 c.c. of alcohol up to 100 c.c. had been ingested showed no percentage variations greater than the normal except the record obtained after the first 20 c.c. of alcohol, which record does present possibly significant changes.

TABLE IV. *Percentage variations from the normal of records of subjects following the ingestion of various amounts of alcohol*

Intervals	20 c.c.	40 c.c.	60 c.c.	80 c.c.	100 c.c.	120 c.c.	
0.5 sec.	3.3	3.3	1.0	1.0	3.3	...	
1.0 "	7.0	9.8	1.3	1.3	4.0	...	
1.5 "	10.0	20.0	6.6	6.6	6.6	...	
2.0 "	8.0	12.0	0.0	0.0	0.0	...	
2.5 "	2.3	2.3	2.3	7.0	2.3	...	Subj. HOJ
3.0 "	4.7	4.7	0.0	0.0	2.0	...	
3.5 "	5.0	0.0	5.0	2.0	0.0	...	
4.0 "	0.0	0.0	0.0	0.0	0.0	...	
5.0 "	0.0	0.0	0.0	0.0	0.0	...	
0.5 sec.	1.0	5.7	2.3	5.7	2.3	...	
1.0 "	0.0	7.0	5.0	2.7	8.0	...	
1.5 "	6.0	9.0	6.0	3.0	6.0	...	
2.0 "	2.0	4.0	4.0	8.0	8.0	...	
2.5 "	2.0	6.8	13.6	13.6	9.0	...	Subj. RP
3.0 "	5.0	12.5	15.0	20.0	15.0	...	
3.5 "	5.0	13.0	15.8	26.3	21.0	...	
4.0 "	7.8	15.8	15.8	26.3	21.0	...	
5.0 "	20.0	15.8	15.8	23.6	21.0	...	
0.5 sec.	1.0	3.0	...	6.0	3.0	3.0	
1.0 "	2.5	3.8	...	2.5	7.7	2.5	
1.5 "	4.5	4.5	...	7.3	9.0	3.0	
2.0 "	1.0	1.0	...	1.0	5.0	1.0	
2.5 "	0.0	8.7	...	4.3	8.7	4.3	Subj. CCJ
3.0 "	0.0	7.0	...	7.0	11.9	9.5	
3.5 "	0.0	7.0	...	7.0	9.5	9.5	
4.0 "	0.0	12.5	...	12.5	15.0	15.0	
5.0 "	0.0	12.5	...	12.5	15.0	15.0	

VII. Summary and conclusions. The main points of interest in this investigation of pupillary reflex activity centered about the results obtained when two forms of stimuli were used to disrupt the normal equilibrium of the iris musculature or the normal balance between the activation from the sympathetic and the parasympathetic nervous system respectively. One form of stimulation was light and the other form was extra-photic in nature—painful and emotional stimuli and alcohol.

1. All subjects under normal conditions showed that the minimal diameter of the pupil was reached in less than five seconds. The records of the subjects in this study revealed that the average normal pupil contraction time was 3.7 sec. The mode was 3.5 sec. and the range was from 2.0 sec. to 5.0 sec. With respect to the latent period the records revealed that the length of time after light stimulation to the initiation of contraction was on the average .1875 sec., the mode being .20 sec. and the range being from .12 sec. to .25 sec.

2. There was a tendency for the pupil of the persons subjected to painful stimuli before, or simultaneously with, exposure to light to show a more prompt initial contraction immediately following the latent period. This does not support the statement of *Weiler* (46) who maintained that a dilatation of the pupil may be provoked by painful impressions but does support the findings of *Löwenstein* (29) who stated that a painful prick did not inhibit the reaction of the pupil to light. Outside of the findings mentioned the general results obtained from these subjects confronted with painful stimuli presented no consistent changes.

3. All persons except one, who were subjected to emotional stimuli before, or simultaneously with, exposure to light, showed that the normal response of the pupil to light was inhibited. The diameter of the pupil, at the instant that the light stimulus came on, was larger than normal, the latent period was longer, the reaction subsequent to the latent period was more extensive and the pupil took a much longer time to reach its normal minimal diameter. *Löwenstein* (29) found that the simultaneity of two forms of stimuli, light and emotional, caused the pupil to decrease

in stages or steps, remaining for a brief time on a level before decreasing further. This effect he called 'cascade,' a characteristic of the emotional pupillary reaction. In the present study the 'cascade' effect was evident even in some subjects' records under normal conditions and was not so pronounced in the records of the subjects affected by emotional stimuli, that it may be called a characteristic emotional pupillary reaction.

4. When a painful or an emotional stimulus was introduced at the time following the light stimulus when the pupil had apparently reached its minimal diameter, the pupil exhibited a fluctuation in size over a small range.

5. The subjects who ingested alcohol exhibited in their records inconsistent results in pupillary reflex activity. One subject after 20 c.c. of alcohol and two subjects after 40 c.c. of alcohol had been ingested showed a more prompt initial contraction. This finding is the same as that of *Weiler* (46) in three of five of his subjects. Following the ingestion of more alcohol, however, the pupil returned in contraction time, diameter and latent period to approximately the normal in two cases out of three. After the ingestion of still more alcohol, the pupil exceeded the normal in these three respects in two subjects. After 40 c.c. of alcohol, the minimal normal diameter was never reached for two of the three subjects. The pupils of these two subjects showed the minimal pupil diameter which was .4 mm. and .5 mm. above normal to be reached approximately in the normal rate of contraction. This fact indicates a tendency for alcohol to stimulate the sympathetic nervous system sufficiently to maintain a slight pupillary dilatation even under a strong light, besides, of course, acting as a depressant on the parasympathetic nervous system. Further, these same two subjects showed an increase in the latent period after the ingestion of 80 c.c. of alcohol.

6. All records showed that irrespective of the kind or amount of extra-photoc stimulation the pupil reacted to light with contraction. This statement is supported by anatomical facts (9) (33) which reveal that the contraction mechanism is older both phylogenetically and ontogenetically than the dilatator mechanism.

Bibliography

1. ADRIAN, E. D., and FORBES, A. The all-or-nothing response of sensory nerve fibers, *J. Physiol.*, 65, 1922, 301-330.
2. BLAKESLEY, T. H. A means of measuring the apparent diameter of the pupil of the eye, in very feeble light, *Phil. Mag.*, 20, 1910, 966-969.
3. BLANCHARD, J. The brightness sensitivity of the retina, *Phys. Rev.*, 11, 1918, 81-99.
4. BRUBAKER, A. P. A text-book of human physiology. Philadelphia: Blakiston, 1929.
5. BYRNE, J. Afferent relations of the skin and viscera to the pupil dilator mechanism, *Amer. J. Physiol.*, 65, 1923, 482-490.
6. CASON, H. The conditioned pupillary reaction, *J. Exper. Psychol.*, 5, 1922, 108-146.
7. CHAFFEE, E. L., BOVIE, W. T., and HAMPSON, A. The electrical response of the retina under stimulation by light, *J. Opt. Soc. Amer.*, 7, 1923, 1-43.
8. COBB, P. W. Dark-adaptation, *Psychol. Rev.*, 26, 1919, 428-453.
9. COLLINS, E. T. Evolution of the pupillary reactions, *Lancet*, 2, 1924, 583-588.
10. DASHIELL, J. F. Fundamentals of objective psychology. N. Y.: Houghton Mifflin, 1928.
11. DUNN, J. I. The primary pupillary response to light, an autonomic reflex, *Arch. Opth.*, 46, 1917, 193-209.
12. FERREE, C. E., RAND, G., and HAUPT, I. A. A method of standardizing the color value of the daylight illumination of an optics room, *Amer. J. Psychol.*, 31, 1920, 77-86.
13. FERREE, C. E., and RAND, G. An instrument for measuring the breadth of the pupil, *Amer. J. Psychol.*, 38, 1927, 292-293.
14. FERREE, C. E., and RAND, G. Intensity of light and speed of vision, *J. Exper. Psychol.*, 12, 1929, 363-391.
15. FERREE, C. E., and RAND, G. Intensity of light and speed of vision, *J. Exper. Psychol.*, 13, 1930, 388-422.
16. FERREE, C. E., and RAND, G. Relation of size of pupil to intensity of light and speed of vision, and other studies, *J. Exper. Psychol.*, 15, 1932, 37-55.
17. FRENCH, J. W. The unaided eye, *Trans. Opt. Soc.*, 20, 1919, 209-236.
18. FRY, F. R. The rebounding pupil, *J. Nerv. & Ment. Dis.*, 40, 1913, 437-438.
19. GRADLE, H. S., and ACKERMAN, W. The reaction time of the normal pupil, *J. Amer. Med. Assoc.*, 99, 1932, 1334-1336.
20. GRADLE, H. S., and EISENDRATH, E. B. Die Reaktionszeit der normalen Pupille, *Klin. Monatsbl. f. Augenheilk.*, 71, 1923, 311-313.
21. HALLIBURTON, W. R. A text-book of physiology. London: John Murray, 1924.
22. HARTRIDGE, H. Physiological limits to the accuracy of visual observation and measurement, *Phil. Mag.*, 46, 1923, 49-79.
23. HECHT, S. The dark adaptation of the human eye, *J. Gen. Physiol.*, 2, 1920, 499-517.
24. HELMHOLTZ, H. L. F. Handbuch der Physiologischen Optik. (Ed. by James P. C. Southall.) Opt. Soc. Amer., 1924-25. Three volumes.
25. INGRAM, W. R., RANSON, S. W., and HANNETT, F. I. Pupillary dilatation produced by direct stimulation of the tegmentum of the brain-stem, *Amer. J. Physiol.*, 98, 1931, 687-691.

26. KLEEFELD, G. Physiologic and pathologic pupillometry, *Ann. d'Ocul.*, 158, 1921, 262-304.
27. LEBENSOHN, J. E. Oculovisceral reflexes, *Amer. J. Ophth.*, 12, 1929, 562-568.
28. LIEBEN, S., and KAHN, R. H. Die emotionelle Reaktion der Pupille, *Pflüger's Arch.*, 225, 1930, 699-705.
29. LÖWENSTEIN, O. Über die Variationsbreite des Lichtreflexes und der Psychoreflexe der Pupillen, *Arch. f. Psychiat. u. Nervenkr.*, 82, 1928, 285-314.
30. LÖWENSTEIN, O., and WESTPHAL, A. Kinematographische Untersuchungen über Störungen der Pupillenbewegung mit besonderem Hinblick auf den sogenannten Spasmus mobilis, *Arch. f. Psychiat. u. Nervenkr.*, 82, 1928, 315-330.
31. LUTZ, A. Über einige weitere Fälle von binasaler Hemianopsie, *Arch. f. Ophth.*, 125, 1930, 103-124.
32. LUTZ, A. The light pupillary reflex, its path, and its abolition called immobility of the pupil to the light reflex, etc., *Arch. f. Ophth.*, 47, 1918, 266-294; 370-400.
33. MANN, I. C. The development of the human eye. Cambridge: Univ. Press, 1928.
34. MORGAN, J. J. B. The psychology of abnormal people. N. Y.: Longmans Green, 1928.
35. NUTTING, P. G. The retinal sensibilities related to illuminating engineering, *Trans. Illum. Eng. Soc.*, 11, 1916, 1-17.
36. RANSON, S. W. The anatomy of the nervous system. Philadelphia: Saunders, 1931.
37. REEVES, P. The effect of various physical stimuli on the pupillary area and retinal sensibility, *J. Frank. Inst.*, 184, 1917, 717-719.
38. REEVES, P. The minimum radiation visually perceptible, *Astrophys. J.*, 46, 1917, 167-174.
39. REEVES, P. Rate of pupillary dilation and contraction, *Psychol. Rev.*, 25, 1918, 330-340.
40. REEVES, P. The response of the average pupil to various intensities of light, *J. Opt. Soc. Amer.*, 4, 1920, 35-43.
41. SCHIRMER, O. Theoretical and practical considerations concerning the pupillary reflex, *The Post Graduate*, 28, 1913, 20-27.
42. SHASTID, T. H. Pupillary phenomena, *Amer. J. Physiol. Opt.*, 4, 1923, 125-144.
43. SOLLMAN, T. A manual of pharmacology. Philadelphia: Saunders, 1926.
44. TROLAND, L. T. The theory and practice of the artificial pupil, *Psychol. Rev.*, 22, 1915, 167-176.
45. WALLIN, J. E. W. Clinical and abnormal psychology. N. Y.: Houghton Mifflin, 1927.
46. WEILER, K. Untersuchung der Pupille und der Irisbewegungen beim Menschen, *Zeits. f. d. ges. Neurol. u. Psychiat.*, 2, 1910, 101-274.
47. ZOETHOUT, W. D. Physiological optics. Chicago: Professional Press, 1927.

SOME NEURO-PHYSIOLOGICAL SOURCES OF ACTION-CURRENT FREQUENCIES

by

DONALD B. LINDSLEY

I. Introduction. An action-current may be thought of as an electrical manifestation of underlying activity of muscle and nerve, *i.e.*, a negative variation or potential occasioned by a chemico-physical process which may be explained in terms of some form of the membrane theory. An action-current wave shows characteristics similar to those of the sound-wave, namely, frequency, amplitude, and wave-form. The latter two characteristics have so far proved to be of relatively little value in the interpretation of nervous and muscular activity: wave-form, because of the lack of applicability of Fourier analysis to a non-repeating pattern; and amplitude, because of variable skin and tissue fluid resistances and the limitation of variability by the all-or-none law in a single unit. On the other hand most of the functional variation in neuro-muscular activity can be accounted for in terms of frequency of the action-currents.

Since frequency has received the main emphasis in action-current studies, it seemed desirable to determine some of its possible neuro-physiological sources and its comparative values in muscle and in nerve.

In a typical reflex arc there are certain factors affecting action-current frequency, among which may be the refractory period of both sensory and motor units (keeping in mind that the refractory period may vary with the intensity of the stimulus), the number of active units, and the time relations of their respective discharges. In addition to these, which are inherent in the reflex arc, there are other factors which are chiefly responsible for action-current frequency and which we shall designate as sources. *Richter* (30), *Adrian and Bronk* (3), and others have shown that

proprioceptive impulses from the contracting muscle form a very definite part of the centripetal impress upon the anterior horn cells in the reflex arc concerned. The centripetal impulses from sources both diverse and related, contralateral and ipsilateral, must also be evaluated. These latter impulses include those from antagonistic muscle groups, from the contralateral counterpart, where there is one, and from other more distantly related muscle groups, which necessarily enter indirectly into the activity of the gross movement of the limb. Included also in this category are the various sensory components such as pain, temperature, and pressure. Finally, the ever-present influence of the higher centers of the central nervous system over the lower subordinate ones must be recognized.

Specifically, this study concerned itself with the influence of three main factors upon action-current frequencies as expressed in a peripheral muscle or nerve: the proprioceptive influence of the sensory part of the arc under consideration, proprioceptive and other influences from the sensory fields of other interrelated arcs, and the influence of the higher centers over the particular arc studied. In addition, in terms of action-current frequency, the functional relationship between muscle and nerve during both reflex and voluntary activity has been studied.

II. Apparatus and procedure. The recording apparatus consisted of two identical, non-interfering, three-stage resistance-coupled amplifiers, a Westinghouse oscillograph, a General Radio low frequency oscillator, and a signal circuit. The two amplifiers were perfectly matched in regard to frequency, intensity, and wave-form (Fig. 1). A special photographic unit carrying Eastman super-speed motion-picture film was used for most of the recording, although photographic recording paper was used for some phases of the study. On all of the records time was recorded in sigma. In all cases the operative procedure was carried out under deep ether anaesthesia and the records were secured under very light ether anaesthesia (20 to 30 min. after the discontinuance of ether).

All of the electrodes used for recording action-currents from exposed muscles and nerves were made of silver and silver-

chloride. Those used on the exposed muscles consisted of wires flattened to give a plate-like surface 2 mm. square and 1 mm. apart. For recording from nerves, the wires were bent to form hooks which would partially encompass the nerve. Except on the immediate recording surface these electrodes were coated with bakelite varnish for insulation and fused into glass tubes which carried the input leads. The electrodes used in connection with recording action-currents from the gastrocnemius muscle of the rat and from the forearm flexors and the quadriceps femoris group in human subjects were brass plates covered with canton flannel which was saturated with concentrated salt solution. Those used for the white and hooded rats were 2 mm. square and

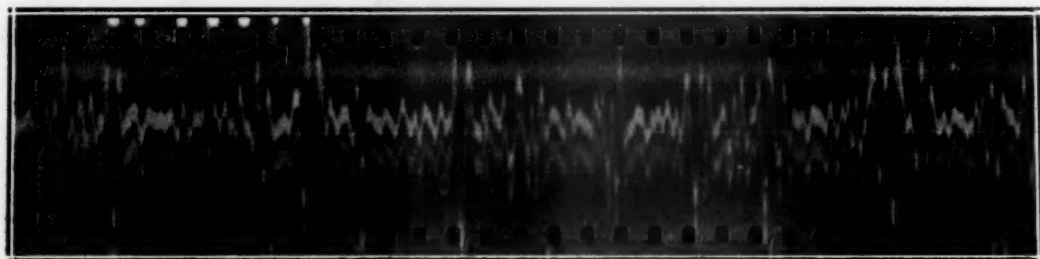


FIG. 1. Record showing the ability of two amplifiers to give perfectly synchronized responses to a single action-current source (forearm muscles) when the input wires to the amplifiers were connected in parallel. The two action-current lines are represented at the bottom. The top line indicates time in σ .

1 mm. apart and those used for human subjects were 5 x 1 cm. For both the human subject and the rat the electrodes were attached as nearly as possible over the motor point of the muscle under consideration. They were curved slightly to fit the curvature of the muscles and were held in place by rubber bands. A Smedley hand dynamometer was used to measure various intensities of contraction of the forearm muscles during voluntary flexion of the digits.

Although additional data in connection with the influence of higher levels upon lower levels of the central nervous system have been taken from studies upon human subjects, most of the results presented in this paper have been derived from experiments involving the Achilles reflex arc of the rat. Further attempts to study the functional relationship between muscle and nerve have

involved the use of the superior laryngeal nerve and the crico-thyroid muscles of the dog, and a sciatic-gastrocnemius rheoscopic heart preparation from the frog.

In all procedures involving the use of the Achilles reflex arc the reflex was elicited by tapping the tendon with a small steel hammer. This hammer constituted one end of the signal circuit which was completed when the hammer struck a small brass plate fastened over, but insulated from, the Achilles tendon. This signal was not absolutely necessary since we were not primarily interested in reflex times. It was useful, however, in differentiating and identifying responses by their temporal relationships. In some cases it was not used due to the tendency of the recording amplifiers to "pick-up", by induction, currents from the signal circuit which was often in close proximity to the lead-off electrodes.

All frequencies presented in this study were taken to include every peak or undulation of the action-current wave during the particular discharge in question. This involved no differentiation of primary and secondary waves or "Nebenzacken".

III. Methods and data: 1. Proprioceptive impulses in the Achilles reflex arc. The Achilles reflex arc of the rat furnished an adequate system for investigating the proprioceptive influences upon action-current frequencies. This reflex arc consists of at least the gastrocnemius muscle, the sciatic nerve, and the corresponding sensory and motor roots with their central connections. The skin and superficial fascia over the popliteal space were incised exposing the internal popliteal nerve. Previous to the use of two amplifiers records were secured from this nerve proximal to its branches to the two heads of the gastrocnemius muscle by placing a pair of hooked electrodes under it and leading off to a single amplifier. Such records were obtained from eight rats, the frequency readings of which are shown in Table I. The sensory and motor discharges were differentiated by temporal factors, as is illustrated in Fig. 2.

In the internal popliteal nerve the sensory discharge usually appeared from .5 to 1.5 σ after the mechanical stimulus to the tendon and was of short duration as it passed along the nerve to

the cord. In reflex activity it was composed of two or three waves which were apparently the result of impulses of proprioceptive origin. Centripetal impulses, such as these, play upon

TABLE I. *Action-current frequencies from the internal popliteal nerve above its bifurcation, from its lateral and medial divisions to the gastrocnemius muscle, and from the lateral and medial heads of the gastrocnemius muscle following Achilles reflex stimulation. Recorded with a single amplifier*

Rat	Internal popliteal nerve						Gastrocnemius muscle	
	Above bifurcation		Lateral division		Medial division		Lateral head	Medial head
	Sen.	Mot.	Sen.	Mot.	Sen.	Mot.		
1	606	739	614	758	653	775	659	749
2	666	710	600	690	702	...
3	583	765	666	739	650	721	697	641
4	619	748	697	817	666	829	700	733
5	666	733	615	756	644	761
6	637	711	647	738	634	716
7	653	748	644	...
8	550	732	652

anterior horn cells in combination with the discharge from upper motor neurones and other interconnecting systems to form the irregular motor impulse discharge which is of greater duration,

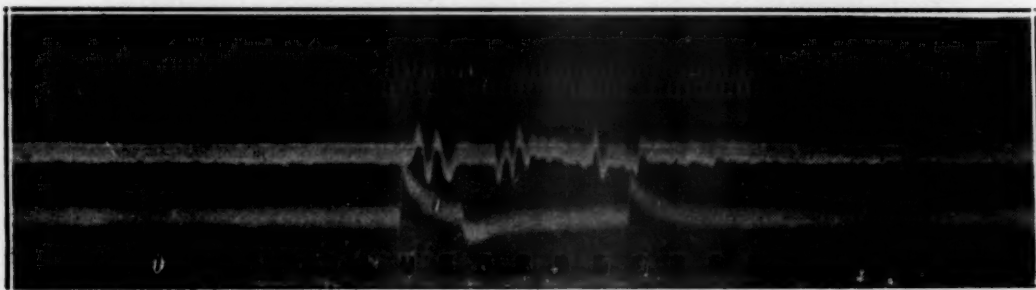


FIG. 2. Action-current record taken from the internal popliteal nerve during Achilles reflex stimulation showing sensory and motor discharges separated by a period of quiescence. Recording by single amplifier. Top line=1000 cycle time line; middle line=action-current line; bottom line=signal line. The first break in the signal line (from left to right) indicates instant of stimulation of Achilles tendon.

amplitude, and frequency. In the internal popliteal nerve the motor discharge appeared suddenly 4 to 5 σ after the termination of the sensory discharge. The total time elapsing between the tapping of the tendon and the appearance of the motor discharge was in the neighborhood of from 6 to 9 σ . This latency is com-

posed of the receptor time, the conduction time in both afferent and efferent fibers, and the "reduced reflex time".¹

This method of recording with one amplifier was of value for studying the sensory and motor discharges during reflex activity, but would be of little value for recording voluntary response due to the overlapping of such discharges. However, for the reflex it amounted practically to a simultaneous recording of the discharges of such a response. In terms of the temporal relationships involved, the validity of this technique has been demonstrated by *Herren and Lindsley* (16). Since other aspects of the study necessitated simultaneous recording, it was deemed advis-



FIG. 3. Action-currents recorded simultaneously from the sensory and motor roots of the fourth lumbar nerve. The break in the first line at the top shows the instant of stimulation of the Achilles tendon. The second line gives time in σ . The third line shows the motor discharge (action-currents) appearing a few σ after the sensory discharge shown in the bottom line.

able to bring two perfectly matched amplifiers to serve in this investigation of the proprioceptive influences within the reflex arc and thus further check the results of the preceding technique with one amplifier.

An incision was made through the sacro-spinal muscle mass at the level of the fourth lumbar nerve. The spinous processes and laminae were removed and the dura mater incised, allowing access to the sensory and motor roots of this nerve. Two pairs of hooked electrodes placed gently under the sensory and motor roots led off the sensory and motor discharges respectively, which were transmitted to the amplifiers and thence to the oscillograph elements which recorded them as separate records on the film. A

¹ "Reduced reflex time" refers to the difference in time between the appearance of the sensory discharge in the sensory root and the appearance of the motor discharge in the motor root, *e.g.*, the amount of time it takes a reflex impulse discharge to pass through the spinal cord.

sample of such a record is shown in Fig. 3. The results of this recording from the sensory and motor roots of the fourth lumbar nerve of ten rats during the elicitation of the Achilles reflex are given in terms of action-current frequencies in Table II. It will

TABLE II. *Action-current frequencies recorded simultaneously from the sensory and motor roots of the fourth lumbar nerve, and from the internal popliteal nerve and the gastrocnemius muscle*

Rat	Fourth lumbar nerve		Internal popliteal nerve	Gastrocnemius muscle
	Sensory root	Motor root		
1	648	846	759	657
2	656	840	776	676
3	639	794	630	527
4	496	682	666	571
5	652	550
6	644	815	736	603
7	622	761	685	526
8	541	363
10	500	638
12	579	673
14	600	666	666	450
15	634	755
16	784	482
17	580	744

be noted that these results verify those of the preceding technique with one amplifier and also that both systems of recording show the same characteristics for the two types of discharge, namely, a greater frequency, amplitude and duration of the motor discharge than of the sensory discharge.

Of interest also was the recording of action-currents from the internal popliteal nerve above the division or bifurcation of this nerve to the lateral and medial heads of the gastrocnemius muscle and also directly from these divisions. The characteristics of the discharge in these two branches, *i.e.*, frequency, duration, and amplitude, were practically the same as in the internal popliteal proximal to these divisions. This appears to be evidence in favor of pluri-segmental innervation of individual muscle fibers as suggested in a diagram by *Lederer* and *Lemberger* (26). Since the gastrocnemius is a plurisegmentally innervated muscle, at least it gives indication of an analogous plan for the innervation of the two heads of the gastrocnemius. Further evidence for the pluri-

segmental innervation of the gastrocnemius will be presented in a succeeding section.

2. *The influence of interrelated arcs upon action-current frequency in the Achilles reflex arc.* By the operative procedure previously described the sensory and motor roots of the fourth lumbar nerve were exposed. Two pairs of hooked electrodes, one under each root, led off action-currents during Achilles tendon stimulation. Leaving the electrodes in the same position on the sensory and motor roots of the fourth lumbar nerve the other ipsilateral nerves which compose the sciatic plexus or join with the sciatic nerve (determined by electrical stimulation) were severed at their point of entrance to the spinal cord. Records were then taken during the elicitation of the Achilles reflex. To further isolate this arc and eliminate still other possible influences playing upon it, all of the contralateral nerves concerned with crossed flexion or extension were severed. Frequency readings from six rats serving in this phase of the study are presented in Table III.

TABLE III. *Action-current frequencies from the sensory and motor roots of the fourth lumbar nerve during elicitation of the Achilles reflex with all ipsilateral and contralateral roots intact; with either all the other both ipsilateral and contralateral roots of the sciatic plexus cut, or with only all the other ipsilateral roots cut. Simultaneously recorded with two amplifiers*

Rat	Normal		Ipsilateral roots cut		Ipsilateral and contralateral roots cut	
	Sensory root	Motor root	Sensory root	Motor root	Sensory root	Motor root
18	647	770	624	789	664	787
19	579	673	590	689	593	661
20	620	724	601	710	609	735
21	639	770	694	783	632	772
22	634	755	620	750	625	768
23	633	738	642	721	687	851

It will be noted that with one exception (rat 23) the frequencies obtained from the sensory and motor roots of the fourth lumbar nerve with either the ipsilateral or the ipsilateral and contralateral roots cut were practically the same as those from the sensory and motor roots of the fourth lumbar nerve with all the ipsilateral and contralateral nerves intact. This may mean that one or more of these segmental roots is capable of maintaining independently the

contraction of the gastrocnemius muscle. *Panizza* [*Fulton* (12) p. 180] suggested such a "community of function" among motor nerve-roots. He believed that each motor nerve-filament of a nerve-plexus was capable of maintaining the motor function of the whole plexus and that the purpose of a number of roots was for alternative pathways in case of injury. *Kronenberg* [*Fulton* (12) p. 181] has added additional evidence to this belief in his finding that excitation of a single root of the brachial plexus caused contraction of practically all the muscles of the limb. We have found also that action-currents taken successively from the sensory and motor roots of the third, fourth, and fifth lumbar nerves during Achilles reflex stimulation are of very nearly the same frequency. The action-currents from any one of these roots with the others cut showed the same frequency. The muscle action-current frequency under these varying conditions remained practically the same. This would seem to be further evidence of the possible individuality of function of the roots concerned with the innervation of the gastrocnemius muscle and also of the plurisegmental nature of this innervation. To a certain extent artificial stimulation with an induction-coil of any of the above mentioned roots caused contraction of the gastrocnemius muscle. Similarly also stimulation of the central cut ends of either the third or fourth lumbar nerves with the fifth remaining intact produced activity of the gastrocnemius muscle. It seems that these facts argue for the possible independent functioning of these three arcs but indicate that there is a close relationship between them which may become one of mutual dependence in case of injury or perhaps under prolonged stimulation. That a subtle effectual relationship between these different arcs did exist might be suggested from the exceptional case, rat 23, in which there was a decrease in frequency with the ipsilateral roots cut and an increase in frequency with the contralateral and ipsilateral roots severed.

3. *The relationship between higher and lower levels of the central nervous system and the resulting effect upon action-current frequencies in peripheral muscles when the relationship is altered.* The dominance of the phylogenetically more recently acquired

higher levels over the lower subordinate ones is a generally accepted fact. To examine this concept further and to determine to some extent its influence on the frequency in peripheral action-current patterns we have proceeded in two directions. First, we produced a general but temporary reduction of higher center control in human subjects by common clinical methods such as the administration of alcohol and the induction of hypnosis. These methods gave the general effect of a reduction in higher center control during voluntary activity. Second, we sought to reduce more or less permanently higher center control in rats by the experimental production of lesions in the cerebral cortex and by transection of the spinal cord.

(a) *Cortical destruction in rats.* After a suitable opening had been made in the skull destruction of cerebral tissue was accomplished by electro-cautery. Since these same animals were used in a learning experiment the areas destroyed were dictated largely by that experiment. The delimitation of the destruction by histological section will be presented at a later date. For our purposes, however, the gross determination of the area destroyed will be sufficient. Diagrams with the respective areas of destruction plotted are shown in Fig. 4. The handedness of these rats had been tested² and the area of destruction was always in the determined dominant hemisphere. By comparing the diagrams in Fig. 4 with those in Fig. 5 the loci of the ablations can be determined.

Action-current frequencies were obtained from the gastrocnemius muscle during elicitation of the Achilles reflex before the operation. Two days following the operation, when all the effects of shock had apparently disappeared and the animals were again active, and at successive monthly intervals thereafter, records were taken. The frequency readings derived from these records are given in Table IV. Unfortunately records were taken before the operation only from the left gastrocnemius muscle during the elicitation of the Achilles reflex. Consequently there are no

² In determining the handedness of the rats we followed the method described by Tsai, L. S., and Maurer, S., "Right-handedness" in white rats, *Science*, 72, 1930, 436-438.

normal right Achilles records for comparison with the right Achilles records following the operation. This may not be such a serious omission, however, as far as our results are concerned,

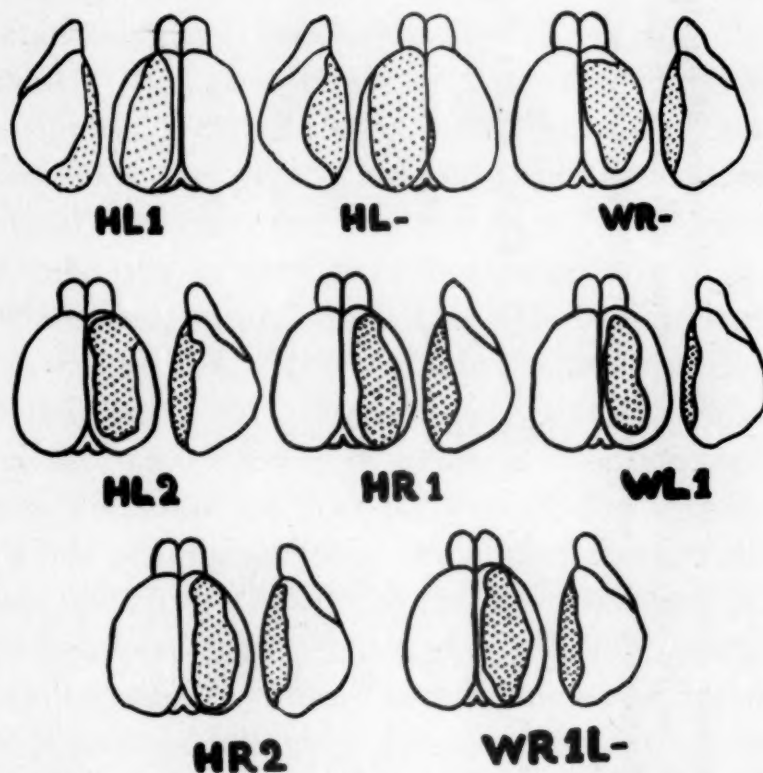


FIG. 4. Diagrams of the rat's brain (superior and lateral views) showing in the stippled areas the extent of destruction in each rat's brain by electrocautery.

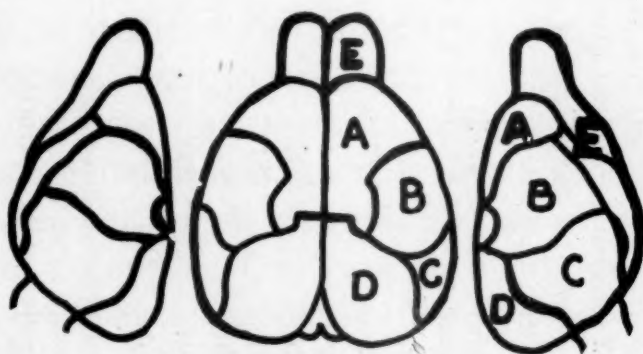


FIG. 5. Diagram of rat's brain (modified from Fortuyn). A = motor area; B = sensory area; C = auditory area; D = visual area; and E = olfactory area.

since only in the case of two animals was there destruction of the left cerebral hemisphere which directly involved the right Achilles reflex arc. Furthermore, by comparison of the right Achilles records in these two rats after the operation with those from the

TABLE IV. Action-current frequencies from the gastrocnemius muscle of the rat during the elicitation of the Achilles reflex. Normal left reflex records before the operation; left and right reflex records at various intervals after the operation in which various portions of the dominant cerebral hemisphere were cauterized. The cauterization was performed on all animals Dec. 28, 1932.

Rat	Hemisphere cauterized	12/27/31		12/30/31		1/27/32		3/1/32		4/1/32		5/3/32	
		LRBO*		LRAO	RRAO	LRAO	RRAO	LRAO	RRAO	LRAO	RRAO	LRAO	RRAO
WR1L—	Right	465		423	500	450	532	462	508	517	487	550	490
HL1	Left	477		500	400	469	415	506	444	529	500
HL—	Left	491		500	461	(died)							
WL1	Right	500		407	500	427	500	505	530	500	490
WR—	Right	451		404	500	(died)							
HL2	Right	500		400	...	410	...	486	472	500	500
HR2	Right	500		508	...	360	588	400	523	(died)			
HR1	Right	464		414	571	452	545	457	529	500	500

* LRBO Left reflex before operation.
 LRAO Left reflex after operation.
 RRAO Right reflex after operation.

other six rats in which a different hemisphere was cauterized, and also by a comparison of the frequencies at various periods when records were taken, it may be seen that the same results apparently held for the right reflex as they did for the left reflex, for which there was an adequate check with normal records. It is evident from Table IV that the frequency from the left gastrocnemius muscle during the Achilles reflex, in the rats with the right hemisphere cauterized, was greatly reduced from the frequency present in the normal records before the operation. This same situation appeared to be true in the right reflex records from animals with the left hemisphere cauterized. The reduced frequency made its appearance in the first records following the operation and was here also reduced to the greatest extent. It will be noticed that each successive record taken at monthly intervals shows the frequency less decreased until at the end of the fourth month the frequency had again returned to the normal level in all of the rats which were still alive. Assuming that the frequency in the normal records was approximately the same in both the right and left gastrocnemius muscles, we can note an increased frequency in the right reflex records following the operation corresponding somewhat to the decrease in the left reflex records in the rats with the right hemisphere cauterized. In other words, there was a decrease in action-current frequency immediately following the operation in the gastrocnemius muscle on the contralateral side to the hemisphere cauterized, but an increase in action-current frequency in the gastrocnemius muscle on the ipsilateral side. These results seem all the more important in the light of the fact that the handedness of all the animals, except one which was ambidextrous, changed. This may be interpreted to mean that the cerebral dominance likewise shifted from one hemisphere to the other. The shift in handedness along with additional data is to be reported soon by *Herren and Lindsley* (17).

The decrease in action-current frequency from the gastrocnemius muscle immediately following the cerebral destruction on the contralateral side with the subsequent gradual increase of the frequency as time went on to a preoperative value was indicative of an immediate "release phenomenon", that is, a reduction of

cortical control which is normally imposed on lower subordinate centers, followed by a period during which much of the control of higher over lower levels returned. This fact is corroborated by a reduction in reflex latencies in the Achilles reflex arc as will soon be published by *Travis, Herren, and Lindsley (37)*. It is well known in clinical neurology that subsequent to brain lesions there is a readjustment in the functional activity in the neighborhood of the lesion in which the remaining nervous tissue tends to take over the functions of the area destroyed. That such a process of restitution was going on in the injured hemisphere with the consequent restoration of control to that hemisphere seemed evident from the fact that the frequency of action-currents in the muscle contralateral to the injured hemisphere decreased immediately following the destruction but subsequently returned to normal during the succeeding months, whereas in the muscle ipsilateral to the injured hemisphere the frequency immediately increased but during the following months returned again to its normal value. It is quite conceivable that under the influence of the process of restitution the originally dominant but injured hemisphere was incapable of maintaining its dominance and as a consequence the shift of dominance to the opposite hemisphere took place with a resulting change of handedness. Interestingly, however, this change of handedness did not transpire suddenly but was a gradual shift from one hand to the other. The apparent increase in action-current frequency in the gastrocnemius muscle of the side ipsilateral to the operated hemisphere immediately following the operation seemed to indicate that the originally non-dominant hemisphere was then exhibiting an influence greater than before, but one which progressively diminished as was indicated by the diminution in frequency from this ipsilateral muscle paralleling the restoration of control in the originally dominant hemisphere.

(b) *Spinal transection.* Further information concerning the "release phenomenon" has been made possible by work with a 'spinal' rat in which there was produced a general reduction in higher level control of a permanent nature. The rat was made 'spinal' by transection of the cord in the mid-thoracic region.

Left Achilles reflex and crossed flexion reflex records were obtained from the gastrocnemius and tibialis anticus muscles respectively, both before and after the operation. The frequency readings from these records are given in Table V. Here we see that with each successive month the frequency decrease which immediately followed the transection of the cord, became less, until finally at the end of the third month the frequency had again returned to normal. These data, in which the influence of higher centers was cut off entirely, parallel those presented in Table IV which show the result of such reduction following cortical lesion.

TABLE V. *Action-current frequencies from the gastrocnemius muscle of a rat during elicitation of the Achilles reflex and from the tibialis anticus muscle during elicitation of the crossed flexion reflex. Records were taken before the rat was made 'spinal' and at successive intervals thereafter as indicated.*

Date	Left Achilles	Left crossed flexion
Normal records:		
3/1/32	529	499
Postoperative records:		
3/22/32	400	517
4/1/32	444	497
4/6/32	472	500
6/1/32	533	—

Records from both ipsilateral and contralateral sides would probably show the same phenomena since the reduction was general, although as pointed out by *Herren* and *Fossler* (15) the crossed reflex seems not to be affected by a reduction in higher center control. The explanation of the return of the frequency to a normal value can be interpreted on the same basis as that cited above, namely, that restitution has taken place. In this case, however, it amounted to a restoration of control probably to some upper spinal cord level.

(c) *Reduction of higher level control by alcohol.* Intoxication was produced in five subjects by the ingestion of 95% grain alcohol (150–200 c.c.) in solution with "near beer". In three of the subjects, both before and during the state of intoxication action-currents from the flexor sublimis group of muscles were obtained during certain degrees of contraction as indicated by kilogram values on a hand dynamometer scale. The contraction

was maintained in each case for three seconds or less.³ The action-current frequencies were determined for comparable intensities of muscular contraction under both normal and intoxicated conditions. In the other two subjects action-current frequencies were secured from the quadriceps femoris group of muscles during voluntary extension of the foot to the horizontal level both before and during alcoholic intoxication. The results from these five subjects are presented in Table VI. Here it may be noted that for comparable degrees of contraction the action-current frequency was markedly decreased under the influence of alcohol. That this decreased frequency of action-currents under alcoholiza-

TABLE VI. *Action-current frequencies from the forearm flexor group of muscles and from the quadriceps femoris group in human subjects under normal conditions, under the influence of alcohol, and under hypnosis. Each group of contractions was of comparable intensity.*

Subject	Normal		Intoxicated		Hypnosis	
	Forearm flexors	Quadriceps femoris	Forearm flexors	Quadriceps femoris	Forearm flexors	Quadriceps femoris
A	442	379
B	474	455
C	439	403
D	446	405
E	399	348
F	456	421
G	458	412
H	468	421

tion was the result of a temporary reduction in higher center control was apparent. Further evidence in this behalf has been presented by *Travis and Dorsey* (35) and *Herren and Fossler* (15), who found a reduction in reflex response latencies in both human and animal organisms under alcoholic influence. Both pairs of investigators found that the latency returned to normal with the resumption of higher center control.

(d) *Influence of hypnosis on action-current frequency.* Following the methods outlined above, action-currents were obtained in three subjects during the waking state and under deep hypnosis. The results are presented in Table VI. Here also was

³ For matters of technique and general discussion of the relation of action-current frequency to degree of muscular contraction see Travis, L. E., and Lindsley, D. B. The relation of frequency and extent of action currents to intensity of muscular contraction, *J. Exper. Psychol.*, 14, 1931, 359-381.

noted a distinct decrease in frequency of action-currents under the influence of hypnosis. Although no satisfactory explanation of hypnosis was available it seemed possible that it was accompanied by or expressed itself in a general reduction of cortical control. This concept was borne out by the decreased frequency of action-currents found here. The particularly varied influence of special suggestion as reported by *Nevski* and *Syrashchich* (28) and as also found in this study, might indicate that there was also a selective influence operative. This was evident in our own results from the fact that during the same objective contraction the action-current frequency would vary if the suggestion was qualified by such statements as "easy to do" or "difficult to do". *Travis* (34) has found that with special suggestion in hypnosis the reflex latency can be reduced significantly.

4. *The relationship between muscle and nerve action-currents.* Our findings, which showed large discrepancies between the frequencies of action-currents from muscle and those from adjacent innervating nerves, have led us to reopen a problem supposedly settled by *Dittler* and *Garten* (8), and *Gasser* and *Newcomer* (13). These workers recorded action-currents from the phrenic nerve and the diaphragm simultaneously and found them of the same frequency and form from both of these structures.

(a) *Gastrocnemius muscle—sciatic nerve relationship in the intact rat.* As shown in Tables I and II the frequency of action-currents from the sciatic nerve at the internal popliteal space was significantly greater than that from the gastrocnemius muscle during reflex activity. Table I in particular shows that this relationship existed between the branches of the internal popliteal nerve and the respective heads of the gastrocnemius muscle. During voluntary activity this relationship between the two structures mentioned has been even more pronounced.

(b) *Cricothyroid muscle—superior laryngeal nerve relationship in the intact dog.* Action-current records, taken simultaneously from the left cricothyroid muscle and from the left external superior laryngeal nerve of a dog during the voluntary activity of whining, showed that the frequency from the nerve was substantially higher than that from the muscle. Of interest in this con-

nection was the fact that the action-current frequencies from the two cricothyroid muscles were the same during this activity.

(c) *Sciatic nerve—gastrocnemius muscle rheoscopic heart preparation of the frog.* In the frog, a rheoscopic heart preparation was made leaving the gastrocnemius muscle with its normal attachments intact so that it might contract under comparatively isometric conditions. This preparation was arranged in clamps so that it was held stationary and rigid although still allowed the freedom of movement necessary to the extension of the foot occasioned by contraction of the gastrocnemius. By means of the hooked electrodes under the sciatic nerve and the plate electrodes on the belly of the gastrocnemius muscle action-currents

TABLE VII. *Action-current frequencies from the sciatic nerve and the gastrocnemius muscle in frogs. Action-currents from the contracting heart muscles (rheoscopic heart preparation) provided the intermittent stimuli.*

Frog	Sciatic nerve	Gastrocnemius muscle
A	948	604
B	862	533
C	806	500
D	739	475
E	819	531

were taken simultaneously from these two structures. Contraction of the gastrocnemius was caused by the action-currents from the contracting heart which were led into the muscle by the nerve. This preparation was used to fulfill the need of an artificial stimulus to a nerve-muscle preparation, since an ordinary induction stimulus to the nerve in the proximity of the amplifier electrodes would be apt to interfere with the amplification of the action-current waves. The results presented in Table VII show the frequency of action-currents from the nerve to be much greater than that of the action-currents from the muscle.

All of these lines of evidence point to the conclusion that during both voluntary and reflex activity the frequency of action-currents from muscle and nerve is not the same but that there is a higher frequency in the nerve than in the muscle.

IV. Discussion. Proprioceptive impulses originating in the end-organs of the muscle as the result of an initial stretching or shortening of the muscle apparently furnish the bulk of the sen-

sory discharge which impinges upon the anterior horn cells. We must not overlook the fact that the sensory discharge may be composed of impulses of both excitatory and inhibitory nature from both the sensory end-organs under immediate consideration and from other sensory end-organs in the animal. That the sensory discharge had been augmented was evident from the difference of frequency in it and in the motor discharge. Whether this augmentation was due to impulses from higher centers and interrelated arcs or to branching paths in the spinal cord [*Forbes* (11)] which tend to spread out the afferent impulses is a problem difficult of analysis. Since, however, we have found in such situations as we have investigated that the effect of interrelated arcs was practically negligible as far as a direct contribution to the motor discharge was concerned, it becomes apparent that the increased frequency in the motor discharge was a function of the influence of the higher centers and the various branchings of the afferent and interconnecting neurones in the cord. We are inclined to agree with the assumption of *Forbes* (11) and others that individual impulses follow different and branching paths in the cord which are of varying length and conductive capabilities. Finding the sensory discharge to be of lower frequency, shorter duration, and greater regularity than the motor discharge indicated that the greater irregularity of the latter was not due to the serial stimulation of afferent endings but rather to the branching reflex paths in the cord which cause temporal dispersion and asynchronism of impulses.

The findings of the present study support the view that the proprioceptive impulses operate against a background or upon a "set stage" which is capable of great variability. That inhibition operates to control the centrifugal discharges and has its effect somewhere on the efferent side of the arc is evident. It may be of local nature, *i.e.*, within the arc itself, as it is known that there are proprioceptive inhibitors as well as excitors and that there is reciprocal innervation wherever antagonistic muscle groups are concerned. Similarly we must recognize the inhibitory and excitatory effects which operate in connection with crossed reflexes. Lastly, our results show that by interference

with higher center control by cortical destruction, alcohol, hypnosis, and spinal transection a change (reduction) in the frequency of action-currents in the muscle was produced. By "set stage", then, is meant all of the influences, both inhibitory and excitatory, which we have just mentioned, as they impinge upon, or exist in the neighborhood of, the anterior horn cells and leave in their wake such conditions as "subliminal fringe" [Denny-Brown and Sherrington (7), and Sherrington (33)] or analogous inhibitory effects. Other results are recruitment and derecruitment processes in which, under continued excitatory or inhibitory stimuli, the number of active motoneurons is increased or decreased respectively. Still other evidences of contributory influences in the formation of a background against which proprioceptive impulses operate are apparent in such findings as reduced reflex time under conditions causing a reduction of cortical control [Travis, Herren, and Lindsley (37), Travis and Dorsey (35), (36)] or the decreased irritability in the sciatic nerve when severed from its connections with the higher centers of the brain as determined by the chronaxie measurements [Madame Lapicque (25)]. By way of summary we might say that the proprioceptive impulses from the muscle make up the bulk of the centripetal discharge but operate against a background of variable conditions, such as we have just mentioned, which are capable of altering or contributing to the proprioceptive impulses before they appear as a motor discharge on the efferent side of the arc.

In a discussion and review of some of the literature on voluntary electromyograms by Pritchard (29), the underlying basis for action-current rhythms in the periphery is apparently found chiefly in connection with the proprioceptive impulses. Particularly is this true of some of the pathological cases cited, especially those of Weizsäcker (38). He discovered in tabes dorsalis in which the proprioceptive impulses were lost or impaired that the action-current picture was greatly affected. In the completely 'spinal' man the spinal reflexes gave rhythms identical with those from voluntary movements. This may be interpreted as additional evidence for the theory that any action-current frequency or rhythm of peripheral muscles and nerves is a rhythm

inherent in the reflex arc itself, arising from proprioceptive impulses and limited by certain conditions within the arc which in turn are capable of modification by interrelated arcs and higher centers. Some of the conditions within the reflex arc which might limit the ultimate rhythm of the motor discharge are the number of afferent units (end organs and their afferent neurones) excited, plus the refractory period of each and their respective time relations to each other, the amount of temporal dispersion caused by branching paths within the cord before convergence of afferent impulses upon an anterior horn cell, the amount of inhibitory or excitatory influence of higher centers and other arcs imposed also in the neighborhood of the anterior horn cell, and the number of motor neurones excited plus the refractory period of each and their respective time relations to each other. That the rhythm we speak of as inherent within the arc itself is highly variable is evident. Modifying influences imposed on the arc by higher centers and other arcs make it increasingly variable. Whether these latter influences, *e.g.*, excitatory or inhibitory ones, are similar types of discharge which vary chiefly in degree it is beyond the scope of this paper to discuss. Also, whether inhibition may be considered to be of the "interference" type (*Verworn, Wedensky, Lucas, Adrian*, and others) or of the "inhibiting substance" type [*Loewi* and others, cited by *Adrian* (1)] is only indirectly related to the findings of the present study.

Of greater concern here is the explanation of some apparently contradictory findings. *Fulton* (12, p. 79) states: ". . . and various other physiological characteristics have been found to vary according to their chronaxie. Thus the briefer the chronaxie of a given tissue: (a) the more rapid the rate of conduction of the action-current; (b) the more rapid the rate of development of the action-current; (c) the briefer the summation interval for subliminal stimuli; (d) the briefer the refractory period; . . .". In terms of this statement *Madame Lapicque's* (25) finding that the chronaxie of the sciatic nerve increased when cut off from higher center influence is an apparent although not necessarily a real contradiction to our findings [*Travis, Herren* and *Lindsley* (37)], which have indicated that under "release" from higher

center control the reflex-time was decreased. Her finding is in apparent agreement, however, with the fact that we found muscle action-current frequencies reduced under these conditions.

The three measurements, chronaxie of the sciatic nerve of the frog when severed from the higher centers, the reflex latency in the patellar and Achilles reflexes under cortical lesion or alcoholic intoxication [Travis, Herren, and Lindsley (37), Travis and Dorsey (35), (36)], and the action-current frequency in peripheral musculature after similar reduction of higher center control, may not be indications of the same thing. The relationship between chronaxie and the factors intimately related to reflex time and action-current frequency may be as Fulton has stated it but Madame Lapicque's (25) chronaxie measurements apply only to the sciatic nerve whereas reflex time and action-current frequency in the motor nerve or muscle involve variables in other parts of the reflex arc. Therefore we can not assume that these results directly support or contradict each other.

Other findings of significance which are related to those already mentioned are those of Lapicque and collaborators (22), (23), (24). These bear out Lapicque's concepts of "chronaxie de constitution" and "chronaxie de subordination". The latter concept involves a more or less normal flexor-extensor chronaxie ratio of 2:1, whereas the former, the "chronaxie de constitution", brought about by reduction or complete severance of higher center control, causes an equalization or reversal of the normal flexor-extensor relationship. A study throwing further light on this problem was made by Malamud, Lindemann, and Jasper (27). They evaluated the effects of alcohol on chronaxie of peripheral musculature. The chronaxie relationships between flexors and extensors under reduced higher center control suggested possible reasons for the reduced action-current frequencies under similar conditions.

Although both frequencies are supposedly indicative of the motor discharge in the same arc, the discrepancy in action-current frequency in the motor roots and in the internal popliteal nerve (the frequency was higher in the motor roots than in the internal popliteal nerve) which is noticeable in Table II, may be ade-

quately accounted for. We noted that according to *Eccles* and *Sherrington* (9), *Cooper* (6), and others there is a branching or bifurcation of the fibers toward the periphery thus giving a greater number of fibers in the region of the internal popliteal space. This fact alone would tend to increase action-current frequency in the internal popliteal nerve over that in the motor roots. On the other hand *Eccles* and *Sherrington* (9) have found that the size of the fibers varies, there being two groups of fibers, one in the neighborhood of $4\ \mu$ and the other about $14\ \mu$ or $15\ \mu$ in diameter. This necessarily causes the conduction rate to differ [*Gasser* and *Erlanger* (14)] in these two groups of fibers and serves as a modulating factor on the frequency by spreading out the impulses. This condition, plus the fact that all motor fibers tend to decrease in size toward the periphery, probably overcompensates for the tendency to increased frequency occasioned by bifurcation and results in a lower frequency in the internal popliteal nerve than in the motor roots of the same arcs at their point of entrance to the cord.

Lapicque (19), (20), (21), and others have shown a condition of isochronism to exist between muscle and nerve, which might be interpreted to fit in with an "equi-functional" relationship between muscle and nerve as expressed by the findings of *Dittler* and *Garten* (8), and *Gasser* and *Newcomer* (13) in which action-currents from the phrenic nerve and the diaphragm showed the same frequency characteristics. However, we have consistently found a greater action-current frequency in nerve than in muscle. This indicated that very probably the refractory period of the muscle fibers, which is greater than that of nerve fibers, operated as a protective mechanism preventing over-work or strain of the muscle. *Eccles* and *Sherrington* (10) have shown that the refractory period of the neurone is from 10–15 σ which would allow each unit to discharge at a frequency between 66–100 times per sec. Assuming a great number of units are operating in rotational fashion but necessarily overlapping it is not difficult to conceive of the high frequencies with which the refractory period of the muscle has to cope at the periphery.

That our results differ from those of *Dittler* and *Garten* (8)

and Gasser and Newcomer (13) can hardly be explained by the fact that the structures with which they worked operated on a more purely reflex basis, for our results were obtained under both voluntary and reflex conditions. Adrian and Bronk (2) have further suggested that it is unlikely that the innervation of the diaphragm differs much from that of an ordinary skeletal muscle, and that the discharges of other motor neurones will have the same general character as those of the phrenic nerve. They add, however, that a group of motor neurones activated by a center in the brain stem may give a different type of discharge from those activated in a short spinal reflex. They also state that the motor fibers of the phrenic nerve transmit discharges which are almost an exact counterpart of those in the sensory fibers, and that the upper limit of motor discharge of the phrenic is somewhat lower than that from a sensory organ. These latter statements are not in accord with our findings of a greater frequency of the motor discharge (action-currents) than of the sensory discharge. There may then be a different mechanism operative in this more or less automatic reflex (phrenic nerve-diaphragm) which may account for the difference between our findings and those of other investigators on the relationship between muscle and nerve action-current frequencies. The discrepancy might be accounted for, however, by the fact that in more recent times a greater refinement of apparatus has led to a more adequate recording of higher frequencies.

Although Katz (18), Brodman and Cattell (4), Cattell (5), Lederer and Lemberger (26), Samojloff (32), and others have presented evidence both for and against plurisegmental innervation by heat and tension measurements and Samojloff (31) has discovered some evidence against it by electrical response methods, the evidence found in the present study favors the principle of plurisegmental innervation. It seems to lead at least to further possibilities for investigating this relationship. Fulton (12, p. 183) has summarized the situation conservatively in stating that for different muscles and different animals we must expect varied results.

V. Summary. An attempt has been made to determine the source of action-current frequencies as expressed in a peripheral nerve or muscle. By various procedures, involving delimitations of the Achilles reflex arc of the rat and possible influences upon it, we have tried to determine the relative importance of proprioceptive impulses within the arc itself, the effect of related arcs, and the influence of higher centers upon action-current rhythms expressed on the motor side of the Achilles reflex arc. Additional evidence concerning the influence of higher levels of the central nervous system over lower subordinate ones has been drawn from experimentation upon human subjects. Finally the functional relationship between muscle and nerve during voluntary and reflex activity was studied.

1. The motor discharge in the Achilles reflex arc was accompanied by action-currents of greater frequency, amplitude, duration, and irregularity than those accompanying the sensory discharge.

2. The influences, contributed by interrelated ipsilateral and contralateral reflex arcs, on action-current frequency accompanying the motor discharge in the Achilles reflex arc were comparatively negligible in the reflex situations examined, although other well-known phenomena indicate that they may have an inhibitory or excitatory effect.

3. Interference with higher centers or "release" of lower levels from higher center control caused a decreased action-current frequency at the periphery. Destruction of cortical tissue in the dominant hemisphere of the rat caused a shift of handedness (dominance) and an alteration of higher level control which resulted in a decreased frequency of action-currents in the gastrocnemius muscle of the contralateral side and an increased frequency in the gastrocnemius muscle of the ipsilateral side. The frequencies from both gastrocnemii, ipsilateral and contralateral to the area of cerebral hemisphere destroyed, paralleled each other in their return to the normal frequency level during a period of restitution which followed the cortical destruction.

4. Spinal transection provided a subsequent decreased action-

current frequency from the gastrocnemius muscle during the Achilles reflex activity but not in the tibialis anticus muscle concerned in the crossed flexion reflex activity. A period of restitution apparently operated here also to cause the frequency of action-currents to return to the normal pre-operative level.

5. In human beings alcohol and hypnosis caused a diminution in muscle action-current frequency during voluntary contraction.

6. Further evidence in favor of plurisegmental innervation of individual fibers in the gastrocnemius muscle was discovered.

7. The frequency of action-currents in the nerve during both reflex and voluntary activity was higher than that from the muscle it innervated.

8. Proprioceptive impulses resulting from an initially stretched or shortened muscle, subject to variable conditions within the reflex arc and modifying influences outside the arc, *i.e.*, from interrelated arcs and higher centers, provided an inherent rhythm of widely variable dimensions to which the muscle responded only within the limits of its physiological characteristics. They probably serve as protective mechanisms, supplementing the well-known senses of pain, strain, and fatigue.

Bibliography

1. ADRIAN, E. D. Some recent work on inhibition, *Brain*, 47, 1924, 399-416.
2. ADRIAN, E. D., and BRONK, D. W. The discharge of impulses in motor nerve fibers; Part I. Impulses in single fibers of the phrenic nerve, *J. Physiol.*, 66, 1928, 81-101.
3. ADRIAN, E. D., and BRONK, D. W. The discharge of impulses in motor nerve fibers; Part II. The frequency of discharge in reflex and voluntary contractions, *J. Physiol.*, 67, 1929, 119-151.
4. BRODMAN, K., and CATTELL, MCK. Heat vs. tension in relation to the problem of plurisegmental innervation, *J. Physiol.*, 70, 1930, 205-217.
5. CATTELL, MCK. Plurisegmental innervation in the frog, *J. Physiol.*, 66, 1928, 431-442.
6. COOPER, S. The relation of active to inactive fibers in fractional contraction of muscle, *J. Physiol.*, 58, 1923, 209-229.
7. DENNY-BROWN, D. E., and SHERRINGTON, C. S. Subliminal fringe in spinal flexion, *J. Physiol.*, 66, 1928, 175-180.
8. DITTLER, R., and GARTEN, S. Die zeitliche Folge der Aktionsströme in Phrenicus und Zwerchfell bei der natürlicher Innervation, *Zeits. f. Biol.*, 58, 1912, 420-450.

9. ECCLES, J. C., and SHERRINGTON, C. S. Numbers and contraction-values of individual motor-units examined in some muscles of the limb, *Proc. Roy. Soc., B*/106, 1930, 326-357.
10. ECCLES, J. C., and SHERRINGTON, C. S. Studies on the flexor reflex, *Proc. Roy. Soc., B*/107, 1931, 511-605.
11. FORBES, A. The interpretation of spinal reflexes in terms of present knowledge of nerve conduction, *Physiol. Rev.*, 2, 1922, 361-414.
12. FULTON, J. F. Muscular contraction and the reflex control of movements. Baltimore: Williams and Wilkins, 1926.
13. GASSER, H. S., and NEWCOMER, H. S. Physiological action-currents in the phrenic nerve, *Amer. J. Physiol.*, 57, 1921, 1-27.
14. GASSER, H. S., and ERLANGER, J. The rôle played by the sizes of the constituent fibres of a nerve trunk in determining the form of its action potential, *Amer. J. Physiol.*, 80, 1927, 522-547.
15. HERREN, R. Y., and FOSSLER, H. R. Achilles and crossed flexion reflex-time in the intact rat, *Amer. J. Physiol.*, 97, 1931, 282-285.
16. HERREN, R. Y., and LINDSLEY, D. B. Central and peripheral latencies in some tendon-reflexes of the rat, *Amer. J. Physiol.*, 99, 1931, 167-171.
17. HERREN, R. Y., and LINDSLEY, D. B. (MS. in preparation).
18. KATZ, L. N. On the supposed plurisegmental innervation of muscle-fibers, *Proc. Roy. Soc., B*/99, 1925, 1-7.
19. LAPICQUE, L. Nouvelle démonstration de l'égalité des chronaxies entre le muscle strié et son nerf moteur, *C. R. Acad. Sci.*, 180, 1925, 1056-1058.
20. LAPICQUE, L., and M. Curarisation par la vératrine; antagonismes dans la curarisation, *C. R. Soc. Biol.*, 72, 1912, 283-285.
21. LAPICQUE, L., and M. Action locale de la strychnine sur de nerf; hétérochronismes non curarisants; poisons pseudo-curarisants, *C. R. Soc. Biol.*, 74, 1913, 1012-1014.
22. LAPICQUE, L., and M. Modification des chronaxies motrices périphériques par les centres nerveux, supérieurs, *C. R. Soc. Biol.*, 99, 1928, 1390-1392.
23. LAPICQUE, L., and M. La chronaxie de subordination; la regulation réflexe, *C. R. Soc. Biol.*, 99, 1928, 1947-1949.
24. LAPICQUE, L., and KAJIWARA, S. Changements dans les chronaxies périphériques sous l'influence de l'alcool, *C. R. Soc. Biol.*, 105, 1930, 632.
25. LAPICQUE, M. Action des centres encéphaliques sur la chronaxie des nerfs moteurs, *C. R. Soc. Biol.*, 88, 1923, 46-47.
26. LEDERER, R., und LEMBERGER, F. Zur Frage der doppelten Innervation von Muskeln des Warmblüters, *Pflüger's Arch.*, 119, 1907, 95-109.
27. MALAMUD, W., LINDEMANN, E., and JASPER, H. H. The effects of alcohol upon chronaxie of the motor system, *Trans. of Amer. Neurol. Assn.*, 1932 (In press).
28. NEVSKI, I., and SRYASHCHICH, K. Influence of hypnosis on muscular strength, *Nev. refl. fiziol. nerv. sist.*, 3, 1929, 458-486.
29. PRITCHARD, E. A. B. The electromyogram of voluntary movements in man, *Brain*, 53, 1930, 344-375.
30. RICHTER, C. P. On the interpretation of the electromyogram from voluntary and reflex contractions, *Quart. J. Exper. Physiol.*, 18, 1928, 54-77.
31. SAMOJLOFF, A. Zur Frage der doppelten Innervation des Froschgastrocnemius, *Pflüger's Arch.*, 204, 1924, 691-707.

32. SAMOJLOFF, A. Zur Frage der plurisegmentellen Innervation quergestreiften Muskels, *Pflüger's Arch.*, 210, 1925, 641-645.
33. SHERRINGTON, C. S. Some problems attaching to convergence, *Proc. Roy. Soc.*, B/105, 1929, 332-362.
34. TRAVIS, L. E. (Investigation now in process).
35. TRAVIS, L. E., and DORSEY, J. M. Effect of alcohol on the patellar tendon reflex time, *Arch. Neur. & Psychiat.*, 21, 1929, 613-624.
36. TRAVIS, L. E., and DORSEY, J. M. Patellar tendon reflexes in psychiatric and in neurologic cases, *Arch. Neur. & Psychiat.*, 22, 1929, 99-104.
37. TRAVIS, L. E., HERREN, R. Y., and LINDSLEY, D. B. (MS. in preparation).
38. VON WEIZSÄCKER, V. Über Willkürbewegungen und Reflexe bei Erkrankungen des Zentralnervensystems, *Deutsch. Zeits. f. Nervenheilk.*, 70, 1921, 115-130.

A COMPARATIVE STUDY OF THE ACHILLES AND
THE PATELLAR REFLEX RESPONSE LATENCIES
AS MEASURED BY THE ACTION CURRENT AND
THE MUSCLE THICKENING METHODS

by

CLARENCE L. NYSTROM

I. Introduction. Dodge (4) lists three techniques for the measurement of the latent times of the Achilles and the patellar tendon reflexes: (1) the recording of the gross movement of the limb, (2) the recording of the thickening of the executant muscle, and (3) the recording of the currents of action from the executant muscle. He rules out the first of these as being too crude to be of value in the determination of latent time for the reflex, although it has been recently used by Tuttle (19) for recording the extent of the movement of the limb in the patellar reflex, and by Royal (13) to record the latency of the muscle in the intact human gastrocnemius muscle.

Although used by Dodge as early as 1911, the latter two techniques have become more or less standardized within recent years, one or the other of them having been used in practically every study measuring latent times of the deep tendon reflexes. The latencies reported from the use of these two techniques have been at considerable variance, those recorded by the muscle-thickening technique being consistently longer than those recorded by the action-current technique, but there appears to have been no attempt to determine the relationship existing between them by recording the latencies simultaneously from the same point on the muscle by means of the two techniques. This is the problem undertaken in this study.

The results of early workers using the muscle-thickening technique to determine the latent time for the patellar reflex in man have been tabulated by Fearing (8) as follows:

Investigator	Date	Time (σ)
Tschirjew	1879	58-61
Gowers	1879	15-90
Brissaud	1880	50
ter Meulen		35-90
Waller	1880	30-40
James	1880	25
Eulenberg	1882	24
De Watteville	1882	20
Rosenheim	1884	31-33
Jendrassik	1894	23

As pointed out by *Fearing*, much of the divergence in these results was doubtless due to the different methods used.

Using a more refined technique, *Dodge* (4) reported an average of 50 σ for the Achilles reflex and 35 σ for the patellar. *Miles* (11), using *Dodge's* technique, obtained much the same results, reporting a range of 32-35 σ for the patellar reflex. *Rounds* (12) working with the Achilles reflex reported an average latency of 54 σ , with a range from 32-96 σ .

The method of recording the currents of action from the executant muscle was probably first used by *Dodge* (4). The findings of some of the principal workers using this technique in man have been summarized by *Travis* and *Young* (17) as follows:

Investigator	Reflex	Ave. time (σ)	Range (σ)
Wertheim-Salomonsen	Patellar	10.0
Snyder	Patellar	11.3	8-15
Hoffman	Patellar	19-23
	Achilles	31-36
Jolly	Patellar	21.3	20.5-22.7
Dodge	Patellar	14.0
	Achilles	35.0

Here again the differences are probably attributable to the difference in methods used.

Travis (16, 17), using the oscillograph, has reported an average latent time of 31.0 σ , in a range of from 26.0 to 36.5 σ for the Achilles reflex and a mean of 18.9 σ , in a range of from 15.2 to 21.6 σ , for the patellar reflex.

Thus even in the most recent studies presumably using the most refined techniques, a difference of from 15-20 σ will be noticed between the latent times recorded by the two techniques in the same reflex.

For the purpose of determining the latent time of peripheral

striped muscle, physiologists have done a considerable amount of work in the simultaneous recording of action currents and the direct muscle response in the frog. Using a frictionless myograph for recording the direct muscle response in thickening, *Einthoven* (6) showed an essential similarity between the electro- and mechano-grams in the frog. He attributed the suppression of the mechanical response without the disappearance of the electrical phenomenon to the greater sensitivity of the galvanometer. *Fulton* (9), working with the gastrocnemius muscle of the frog (*rana temporaria*) at 20° C and using highly refined techniques, has concluded that the "true" latency of the muscle, *i.e.*, the interval from the first appearance of the electrical response to the first appearance of the mechanical response, is from 1.5–2 σ . In mammals he believes it to be about 1 σ . In addition to this "true" latent time of the muscle he observed a "period of rigidity" which lasted from 4–5 σ before the muscle shortened. He gives the total latent period of the frog's muscle as from 5–7 σ . The period is doubtless somewhat shorter in warm-blooded animals, being according to *Fulton* between 4 and 5 σ .

Burdon-Sanderson (2, 3) and *Erlanger* and *Gasser* (7) have shown that in skeletal muscle the action currents appear simultaneously with the stimulus. In the tendon reflexes we may interpret this to mean that the action currents appear simultaneously with the arrival of the nerve impulses from the reflex centers in the cord controlling the response. *Burdon-Sanderson* concluded from his experiments that mechanical thickening of a given spot on the muscle occurs approximately 2.5–3 σ after a stimulus is applied at the spot.

Buchanan (1) has shown that in the gastrocnemius muscle of the frog, stimulated directly by means of an induction shock, the mechanical response uniformly outlasted the electrical effect, the latter often having terminated before the mechanical response had reached its maximum.

If the findings of these physiologists in respect to the electrical and mechanical responses in the muscle of the frog hold for the muscle groups involved in the intact Achilles and patellar tendon reflexes in the human being, or, indeed, as some of them point out,

the time relationships being probably even shorter, then the large differences between the latent times as recorded by the two techniques mentioned above are doubtless due to imperfections in the muscle-thickening technique, either because of inherent factors or because of lack of refinement. The problem still remains as to whether there is an essentially constant relationship between the latencies as recorded by the two techniques, so that for comparative purposes, either one would be satisfactory if carefully controlled.

The immediate purpose of this study, then, was to devise a technique whereby the reflex latencies as measured by recording the action currents and by recording the mechanical thickening of the executant muscle might be recorded simultaneously from the same point on the muscle and both latencies be read from the same time-line and the same signal-line on the same film. Both the Achilles and patellar tendon reflexes were studied in this manner. The time relationships existing between the latencies as determined by the two techniques should thus be discovered and possibly some light thrown on the physiological relationships of the electrical and mechanical responses in the muscles involved.

II. Apparatus and methods. The apparatus used in this study consisted of an electrical current generator; a three stage, resistance-coupled amplifier; a portable, three element oscillograph; a vacuum-tube oscillator; and a signal circuit. The electrical current generator has been described by *Travis and Hunter* (15). It consists of a light coil, suspended by four narrow strips of dental rubber dam, moving in a magnetic field which activates a standard element of the Westinghouse oscillograph. In the present study this generator was used to record the muscle thickening in the manner to be described later. The remainder of the apparatus has been described by *Travis and Hunter* (16) and by *Travis and Young* (17).

The electrodes for both the Achilles and patellar reflexes consisted of two thin brass strips, about $\frac{1}{2}$ in. x 2 in. and covered with canton flannel, set into thin wooden plates (Fig. 1) in such a manner that the exposed surface of each strip projected slightly beyond the surface of the wooden plate to insure contact with the skin over the muscle. The wooden plate carrying the electrodes for the Achilles reflex was slightly rounded to conform to the shape of the

gastrocnemius muscle and covered the major portion of the muscle. Firmly attached to the back of the wooden plate was a short wooden rod which extended backward and slightly downward. At its end was a polished screw-head which came in contact with the top of the light movable coil. As the muscle thickened during the reflex response the wooden plate was moved by this thickening to depress the coil which in turn, through the field thus generated, activated the oscillograph element. For the patellar reflex the wooden plate was flat, since the muscle is relatively large and the mechanical response greater than in the Achilles reflex. Here the wooden rod extended straight upward since the electrical generator in this case was above the executant muscle. For the Achilles reflex the electrodes were placed on the executant muscle one-fifth of the way between the lower margin of the patella and a point even with the inferior malleolus, and for the patellar reflex on the executant muscle half-way

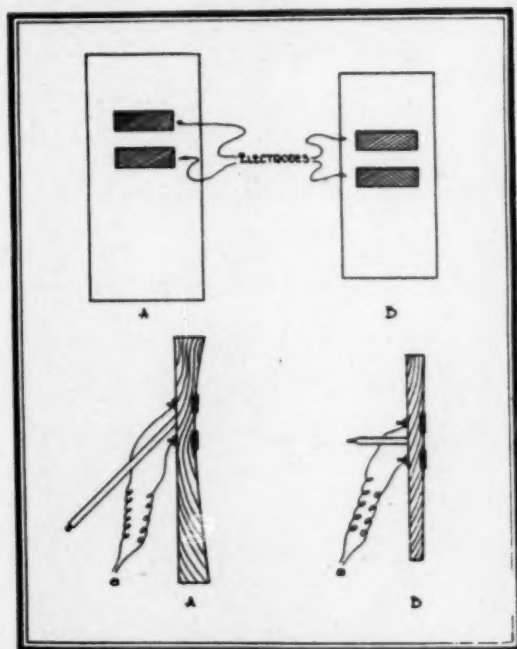


FIG. 1. Electrodes used in recording of latencies. *A* is for the Achilles reflex and *B* is for the patellar reflex.

between the anterior superior spine of the ilium and the upper margin of the patella. During the elicitation of the reflexes the cotton flannel covering the brass strips was kept saturated with concentrated salt solution.

Fig. 2 shows the manner of eliciting and recording the Achilles reflex. The subject was seated in the chair with his right leg back of the wooden bar *A*. A heavy rubber band (*B*) held the leg firmly to the bar. It was found that this band did not in any way affect the reflex latency. A rod with a small bar of wood, *C*, came down from above and prevented any vertical movement of the leg. The sling (*D*) attached to rubber bands (*E*) exerted a slight pull on the foot sufficient to stretch the gastrocnemius muscle slightly. Thus the leg was held firmly, but the apparatus permitted free movement of the foot at the ankle joint when the tendon was tapped. A small iron mallet (*G*) was used to tap the tendon in eliciting both the Achilles and the patellar reflexes. Since Tuttle (20) has shown that the reflex latency is not appreciably affected by the strength of the stimulus, no attempt was made to control the strength of the blow. In both instances the signal-circuit was made upon contact of the

mallet with a small strip of brass held by a light rubber band on the tendon at the point of stimulation. The generator for recording the thickening of the

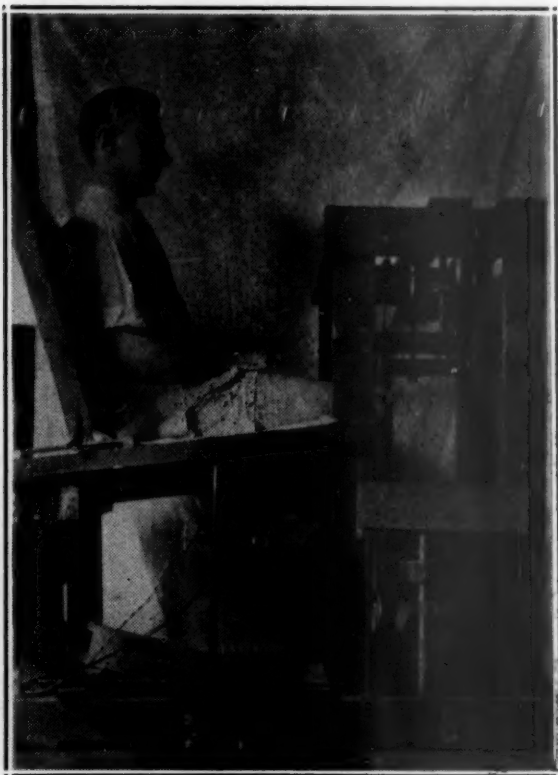
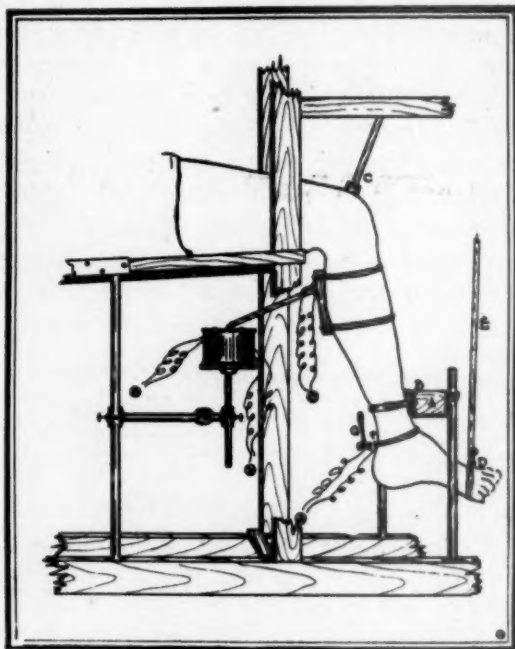


FIG. 2. Apparatus for eliciting the Achilles tendon reflex.

muscle was rigidly supported beneath the chair by means of clamps to hold it to a heavy metal rod firmly attached to the chair. In this way it was freely adjustable in any direction, but it was held immovable when clamped tightly.

As described above, the wooden rod from the wooden plate containing the electrodes came in contact with the light movable coil of the generator and depressed it when the electrodes were moved by the thickening of the muscle in the reflex response. It was observed that the movement of the electrodes was not exactly backward when the reflex was elicited, but rather there was a slightly rolling motion. Thus a maximum of movement at the end of the wooden rod was obtained in an approximately vertical direction. This permitted using the generator in a vertical position.

It was found to be unnecessary to support the leg rigidly in obtaining the patellar reflex. Since the direction of the stimulating blow was at right angles to the direction of movement of the executant muscle, no jar was conveyed to the generator when the tendon was struck, and the weight of the body was

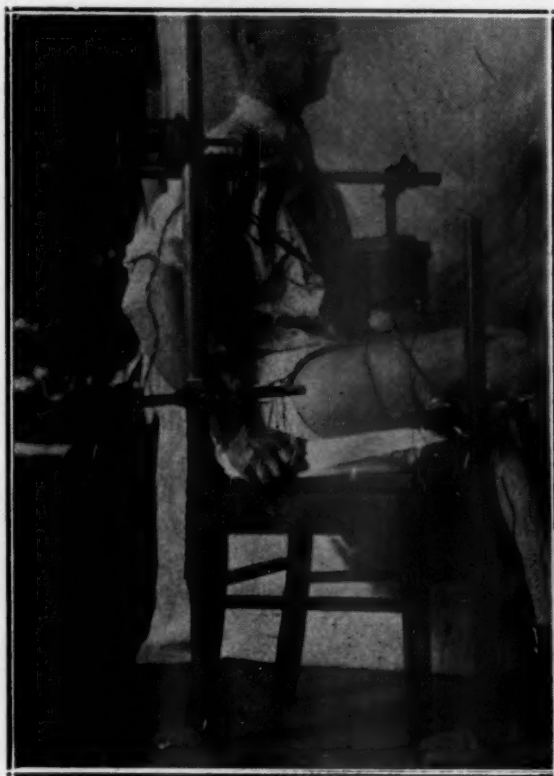


FIG. 3. Apparatus for eliciting patellar tendon reflex.

sufficient to prevent any movement of the upper part of the leg. Fig. 3 shows the method of obtaining the patellar records. The generator (*A*) in this case was supported in an inverted position over the electrode (*B*). The resistance offered by the weight of the coil was probably no greater than that offered by the small rubber bands which supported it in the position used for the Achilles reflex.

Typical records obtained from both the Achilles and patellar reflexes are shown in Fig. 4. From six to ten records were taken from each subject at a single sitting for each of the reflexes, except that for five subjects from 35 to 60 records were taken at a single sitting to determine the constancy of the relation between the action current latency and the muscle-thickening latency over a large series of elicitations of the reflexes. In three subjects the gastrocnemius muscle was fatigued by having the subject first raise the body

on the ball of the right foot repeatedly until he could do so no more and then, while in the chair, push the foot downward repeatedly against the resistance furnished by heavy rubber bands until the muscle was thoroughly fatigued.¹

In the case of the action-current record the time elapsing between the signal deflection and the first deflection of the action-current volley is counted off to the nearest $.5 \sigma$. For the muscle-thickening time the time elapsing between the signal deflection and the beginning of the large deflection of the line following the first smaller and more rapid deflection which is caused by the mechanical stretching of the muscle by the stimulus blow, is counted off to the nearest $.5 \sigma$. Readings were made on all records on which both action-current and muscle-thickening times were clearly readable.

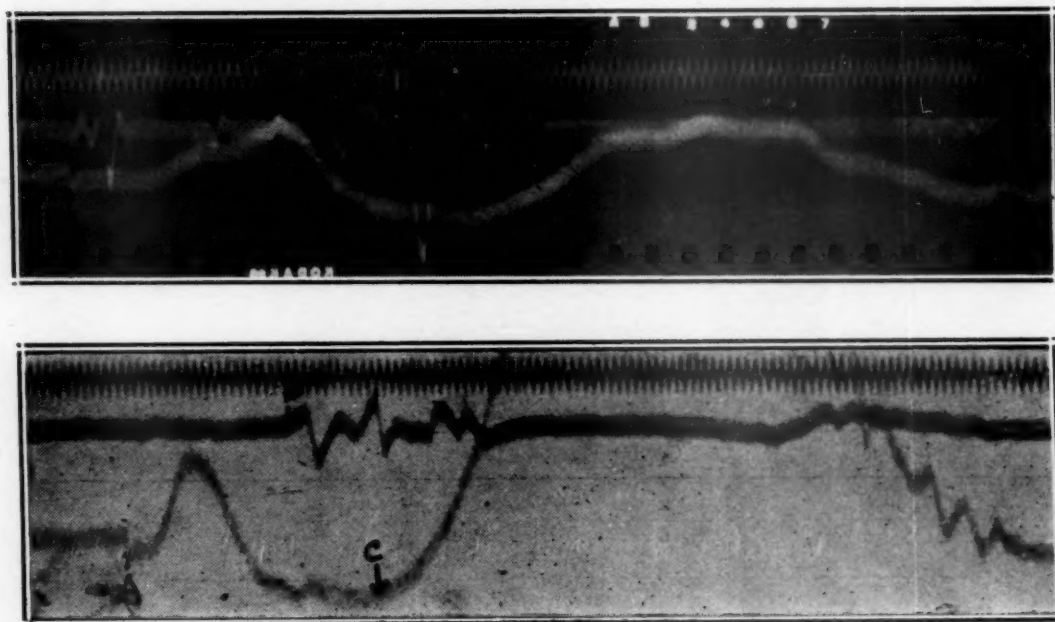


FIG. 4. Typical records from Achilles (above) and patellar (below) tendon reflexes. Lines from top to bottom show: time in σ , action-currents and muscle-thickening response and signal-deflection. In both records *A* shows the instant of striking the tendon, *B* the beginning of the action-current volley and *C* the initiation of the muscle-thickening response.

III. Results. Records of Achilles reflex times were obtained from 45 men and 1 woman. Of these 30 records were readable.² Patellar reflex times were obtained from 34 men, of which 29 records were readable. All of the subjects were undergraduate or graduate students of the university.

¹ That the fatigue was thorough was determined by reports from the subjects, and from observation of the movements of the foot. In two cases the subjects later reported that the muscles of the calf of the leg were sore for two or three days following the experiment.

² The chief reasons for being unable to read records were: (1) damage to the film; (2) outside electrical disturbances; (3) absence of or very weak jerks; and (4) in the case of the Achilles jerk, jar from the blow on the tendon which obscured the beginning of the reflex movement.

From 45 to 60 consecutive Achilles reflex times were secured from five subjects, yielding from 38 to 50 readable measures respectively. Likewise from 35 to 55 consecutive patellar reflex times were recorded, from which 25 to 50 readable measures were obtained respectively. For three subjects records were obtained both before and after the gastrocnemius muscle had been thoroughly fatigued. The records of two of the subjects were readable.

Several records were taken to determine the effect on the time relations when the electrodes were moved a short distance both proximal and distal to the motor point of the muscle, and also the effect of a lighter electrode on the muscle thickening time.

Average reflex times for the Achilles and patellar reflexes. Tables I and II show the average latencies, standard deviations from the mean, differences between latencies as measured by the two techniques, and the ranges of the measures for each subject, together with the means, standard deviations, and ranges of the group. The averages, the standard deviations, and the ranges of the latencies as obtained by the action-current technique were found to be approximately the same as those previously obtained in this laboratory with that technique (16, 17). The averages of the muscle-thickening latencies were found to be somewhat smaller and the ranges decidedly smaller than those reported by other workers using the muscle-thickening technique (4, 11, 12). These differences were probably due to the more highly refined technique employed for recording the muscle-thickening latencies in the present study.

Correlations between latencies as obtained by the two techniques. The coefficient of correlation between the latencies as secured by the action-current technique and those secured by the muscle-thickening technique is shown in Table III for both the Achilles and the patellar reflexes. These coefficients are sufficiently high to indicate that the two latencies are dependent on the same or closely related factors. They likewise suggest that relationships between reflex latency and other factors, *e.g.*, intelligence, speed of mental reactions, height, *etc.*, found to exist when the reflex latency is measured by one technique should also hold

true if the other technique is used. Thus for comparative purposes either technique should give a satisfactory measure of latent time if the techniques used are sufficiently refined. *Travis and Young* (17) have shown that neither the patellar nor the Achilles

TABLE I. *Reflex times, standard deviations, differences between latencies and range differences for Achilles reflex (in σ).*

Subject	Action-current latency	S.D.	Muscle-thicken. latency	S.D.	Difference between latencies	Range	
						Action current	Muscle thicken.
1	29.5	.500	39.5	.500	10.0	1.0	1.0
2	30.8	.897	45.1	.852	14.3	2.0	2.5
3	31.3	.444	41.1	.443	9.8	1.0	1.5
4	31.4	.343	41.4	.449	10.0	1.0	1.0
5	31.7	.400	42.9	.663	11.2	1.0	2.0
6	31.8	.688	40.2	.630	8.4	1.0	1.0
7	31.9	.519	48.2	.990	16.3	1.5	2.5
8	32.0	.447	43.7	.600	11.7	1.0	1.5
9	32.5	.632	42.9	.412	10.4	1.0	1.0
10	32.7	.400	40.7	.926	8.0	1.0	2.5
11	33.0	.612	42.2	.561	9.2	1.5	1.5
12	33.2	.651	46.6	.748	13.4	1.5	2.0
13	33.7	.400	41.8	.509	8.1	1.0	1.5
14	33.7	.748	42.1	.663	8.4	2.0	2.0
15	34.0	.812	42.8	.800	8.8	2.0	3.0
16	34.1	.288	43.7	.435	9.6	0.5	1.0
17	34.1	.833	43.3	1.1160	9.2	2.0	3.0
18	34.3	.374	47.0	.408	12.7	1.0	1.0
19	34.5	.645	47.6	.802	13.1	1.0	2.0
20	34.7	.385	46.3	.800	11.6	1.0	2.5
21	34.7	.748	44.6	.663	9.9	2.0	2.0
22	34.8	.400	47.8	.748	13.0	1.0	2.0
23	34.8	.400	47.2	.509	12.4	1.0	1.5
24	34.9	.489	48.1	.663	13.2	1.5	2.0
25	35.2	.387	47.0	.612	11.8	1.0	2.0
26	35.5	.456	50.8	.746	15.3	1.0	2.0
27	35.8	.472	47.7	.806	11.9	1.5	2.0
28	36.0	.800	53.5	.500	17.5	2.0	1.5
29	36.8	.734	52.5	1.039	15.7	2.0	3.0
30	37.0	.400	52.5	.894	15.5	1.0	3.0
Mean	33.7	.544	45.5	.608	11.8	1.3	1.9
S.D.	1.767		3.752		2.607	.439	.637
Range	29.5- 37.0	.288- .897	39.5- 53.5	.408- 1.160	8.1- 17.5	0.5- 2.0	1.0- 3.0

reflex latencies as measured by the action-current technique correlates with intelligence as measured by standard intelligence tests. On the other hand they have shown that the latencies of these reflexes show high correlations with physical measures that were calculated to be functions of the length of the reflex arc.

The highest correlation was found to be between reflex times and height. *Rounds* (12) has reported a relatively high correlation between reflex times of the Achilles reflex as measured by the muscle-thickening technique and a group of speed tests. While

TABLE II. *Reflex times, standard deviations, differences between latencies, and range for patellar reflex (in σ).*

Subject	Action-current latency	S.D.	Muscle-thicken. latency	S.D.	Difference between latencies	Range	
						Action current	Muscle thicken.
1	16.9	.415	28.6	.415	11.7	1.0	1.0
2	17.5	.534	27.7	.795	10.2	1.5	2.0
3	17.8	.509	28.2	.812	10.4	1.5	2.0
4	18.0	.354	30.7	.561	12.7	1.0	1.5
5	18.1	.786	29.0	1.154	10.9	2.5	3.0
6	18.1	.374	30.8	.678	12.7	1.0	1.5
7	18.2	.479	30.5	.500	12.2	1.5	1.0
8	18.5	.534	31.9	.776	13.4	1.5	2.0
9	18.8	.238	32.4	.447	13.6	0.5	1.0
10	18.8	.472	32.5	.911	13.7	1.5	2.5
11	18.8	.688	30.4	.731	11.6	2.0	2.0
12	18.8	.624	30.8	.688	12.0	2.0	2.0
13	18.9	.519	30.0	.591	11.1	1.5	2.0
14	19.0	.408	31.2	.382	12.2	1.0	1.0
15	19.1	.489	34.1	.583	15.0	1.5	1.5
16	19.2	.538	30.3	.472	11.1	1.5	1.0
17	19.4	.344	31.5	.763	12.1	1.0	2.5
18	19.8	.452	34.0	.597	14.2	1.5	2.0
19	20.0	.463	30.6	.417	10.6	1.0	1.0
20	20.0	.485	35.1	.881	15.1	2.0	2.5
21	20.1	.447	32.6	.867	12.5	1.5	2.0
22	20.2	.559	33.4	.447	13.1	1.5	1.0
23	20.5	.577	35.5	.707	15.0	1.5	1.5
24	20.7	.447	35.0	.550	14.3	1.0	1.5
25	21.0	.563	35.1	.442	14.1	1.5	1.5
26	21.1	.606	35.5	.645	14.4	2.0	2.0
27	21.3	.525	33.8	.525	12.5	1.5	1.5
28	21.5	.378	31.9	.623	10.4	1.0	2.0
29	22.0	.449	36.1	.672	14.1	1.5	2.0
Mean	19.4	.491	32.0	.642	12.6	1.4	1.7
S.D.	1.273		2.323		1.485	.410	.535
Range	16.9-22.0	.238-.786	27.7-36.1	.382-1.154	10.2-15.1	0.5-2.5	1.0-3.0

the factors measured by these latter tests may not be exactly the same as those measured by standard intelligence tests, there is doubtless enough in common between them to warrant the expectation that what is found to be true for one will also be true of the other as far as correlation with reflex latencies is concerned.

Since *Travis* and *Young* (17) and *Hoffmann* (quoted by these authors) have shown quite conclusively that the electromyographically determined reflex time correlates highly with height and length of arc, the findings of *Rounds* are the more surprising, for probably no one would venture to assert that speed of mental reactions correlates with height or length of arc. An examination of the latent times reported by *Rounds* suggests a possible reason for the results obtained by him. He reported latencies ranging from 32–96 σ with a mean of 54 σ . This range and mean are both surprisingly large in view of the times found in the present study. The shortest times obtained by *Rounds* compare favorably with the times obtained in this study by the muscle-thickening technique in the Achilles reflex, but his longest time is almost twice as long as the longest time obtained in this study by that technique, and is probably within the range of voluntary reaction time. It is probable that the technique employed by *Rounds* was not sufficiently refined to give accurate measurements of the reflex response latencies. At least the findings of this study taken together with the findings of *Travis* and *Young* and those of *Hoffmann* cast considerable doubt on the high correlation between speed of mental reactions and the latent time of the Achilles reflex reported by *Rounds*.

TABLE III. *Correlations between latencies as obtained by action-current technique and muscle-thickening technique.*

Reflex	Correlation	P.E.
Achilles.....	.800	.043
Patellar.....	.783	.054

Range as a measure of constant relation. The ranges for both action-current latencies and the muscle-thickening latencies shown in Tables I and II were obtained by finding the difference between the extremes of the measures obtained in each individual case. Since one of the purposes of the study was to determine whether the time relationship between the latencies as obtained by the two techniques, provided the latencies were not identical, was constant or variable, this measure is considered a most satisfactory means of expressing this relationship. The ranges in the tables show that for the Achilles reflex the longest and the shortest latency

obtained in any individual case by the action-current technique did not differ more than 2.0σ , with an average of 1.3σ , and for the muscle-thickening technique not more than 3.0σ with an average of 1.9σ . For the patellar reflex the largest range was found to be 2.5σ , with an average of 1.4σ , for the action-current technique and 3.0σ , with an average of 1.8σ for the muscle-thickening technique.

This essential similarity in the ranges of the measures obtained by the two techniques in any given case is taken to indicate that the action-current latency and the muscle-thickening latency do not vary independently of each other but maintain an essentially constant relationship one to the other.

An inspection of the tables supports the conclusion just advanced by showing that in any given individual the range was approximately the same for either technique. This indicates again that the relation between the latencies as recorded by the two techniques is constant and that the latencies are dependent upon identical or closely and constantly related factors.

Standard deviations from the means as a measure of constant relation. An examination of the standard deviations from the means for each individual case as given in Tables I and II likewise confirms the constancy of relationship between the latencies as obtained by the two techniques. These measures show that the dispersions from the means were approximately the same for the two latencies in any given case. This is particularly striking when it is recognized that the action-current technique is undoubtedly more highly refined and less subject to extraneous influences than is the muscle-thickening technique.

Constancy of relationship between the two techniques over a long series of consecutive measures. It was desirable to determine whether or not the constancy of relationship between the latencies indicated above obtained for a longer series of consecutive measures. The results presented in Tables IV and V are practically identical with those obtained for the shorter series of reflex elicitations. The means of the latency differences were here approximately the same as in the shorter series. The ranges were slightly larger, suggesting that over a long series of consecutive

elicitations of the reflex the factors affecting the variations within a given series probably tend to reach a maximum. The ranges for both latencies were, however, relatively small and it is probable that the extremes were reached in each series. These results indicate that the constant relationship between the latencies as recorded by the two techniques holds true for a long series of

TABLE IV. *Constancy of relationship between two techniques over a long series of measures in Achilles reflex (in σ).*

Case	Action-current latency	S.D.	Muscle-thickening latency	S.D.	Difference in latency	Range	
						A.C.	M.Th.
1	29.3	.457	42.6	.656	13.3	1.5	3.0
3	31.4	.550	43.4	.841	12.0	2.0	3.0
18	34.8	.564	47.1	.686	12.3	2.0	2.5
31	34.5	.490	46.9	.879	12.4	2.0	2.5
32	36.0	.590	47.1	.726	11.1	2.0	2.5
Mean	33.2	.530	45.4	.757	12.2	1.9	2.7
S.D.	2.471		1.993		.708	.200	.244
Range	29.3-36.0		42.6-47.1		11.1-13.3	1.5-2.0	2.5-3.0

TABLE V. *Constancy of relationship between two techniques over a long series of measures in patellar reflex (in σ).*

Case	Action-current latency	S.D.	Muscle-thickening latency	S.D.	Difference in latency	Range	
						A.C.	M.Th.
21	20.9	.566	33.7	.602	12.8	2.5	2.5
2	17.5	.561	27.7	.625	10.2	2.0	2.0
26	20.1	.445	33.8	.576	13.7	1.5	2.0
28	21.6	.609	35.9	.692	14.3	1.5	3.0
33	20.0	.485	35.1	.881	15.1	2.0	3.0
Mean	20.0	.533	33.2	.595	13.2	1.9	2.5
S.D.	1.387		2.889		1.686	.374	.447
Range	17.5-21.6		27.7-35.9		10.2-15.1	1.5-2.5	2.0-3.0

consecutive measures. They also indicate that the shorter series were adequate measures of the relationship.

The influence of peripheral fatigue on the latencies. The muscle-thickening latency is unquestionably dependent on the actual contraction of the muscle itself, whereas the action-current latency is probably dependent on the wave of altered permeability passing over the muscle which is directly caused by the nerve impulses innervating the muscle. For this reason it was thought

that peripheral fatigue of the muscle group involved in the reflex might affect the relationship found to exist between the latencies as recorded by the two techniques, since such fatigue would directly affect the muscle fibers but presumably would not affect the nervous arc of the reflex. Table VI shows, however, that neither reflex latency was affected by such peripheral fatigue in the Achilles reflex. This indicates that the reflex response latency is unaffected by such peripheral fatigue of the executant muscle, assuming that the gastrocnemius muscle was actually fatigued.

TABLE VI. *Effect of peripheral fatigue on Reflex latencies (in σ).*

Case	Action-current latency	S.D.	Muscle-thickening latency	S.D.	Difference in latency	Range	
						A.C.	M.Th.
1	29.6	.374	41.7	.400	12.1	1.0	1.0
3	31.3	.385	43.5	.957	12.2	1.0	3.0

Difference between the latencies as a measure of the latency of the muscle. An examination of Tables I and II reveals further that the muscle-thickening latencies are always longer than the action-current latencies. This doubtless is to be expected, if the view is accepted that the action currents arise from a wave of increased permeability which passes over the muscle when it is stimulated by the nerve impulse innervating the muscle and that the muscle thickening is a result of the mechanical response of the muscle. Since *Erlanger* and *Gasser* (7) have shown that the electrical response appears simultaneously with the stimulus, the difference between the two latencies in a given case should be a measure of the muscle latency. The average difference between the two latencies in the Achilles reflex was found to be 11.8 σ , in a range of from 8.1–17.5 σ ; and in the patellar reflex, 12.6 σ , in a range of from 10.2–15.1 σ . These times are probably somewhat too long to be accepted as the true measures of the muscle latencies. As previously pointed out, *Fulton* (9) gives the probable latent time of human skeletal muscle as about 4.0 to 5.0 σ . *Sherrington* (14) gives similar figures for human beings.

The only study found in the literature which has attempted to measure directly the latent time of intact human muscle is that of *Royal* (13). He stimulated the gastrocnemius muscle by an

induction shock applied at the medial motor point of the muscle and recorded the subsequent movement of the foot by means of a kymograph. He found 22.6 σ to be the mean latent time for this muscle, in a range of from 20.5–25.2 σ . He noted considerable diurnal variation and also individual variation. It will be noted that these times are considerably longer than the latent times for the muscle found in the present study and decidedly longer than those given by *Fulton* and by *Sherrington*. *Royal's* technique is open to criticism, however, if an accurate measure of the latent time of the muscle is desired, for rather than the thickening of the muscle he recorded the gross movement of the foot which as *Dodge* (4) has pointed out is too crude a technique to give an accurate measure of the response latency. It is doubtful, therefore, whether the latent times of the muscle reported by *Royal* can be accepted as more than crude approximations of the true latent time of the muscle measured.

It is probable that the latent times for the muscle found in this study were also affected by extraneous factors that tended to exaggerate them. In the first place, the movable coil of the electrical current generator, while very light, would, together with the rubber bands supporting it, offer some resistance to the thickening of the muscle which would tend to increase the latent time; secondly, because it is probable that a much greater number of muscle fibers must be in contraction to move the wooden plate than is necessary to produce an action-current, the plate may be said to have a cushioning effect on the mechanical response; thirdly, it is entirely possible, and perhaps probable, that the initial movement in the responding muscle may not be in a vertical direction (the direction necessary to move the plate), but in some other direction, perhaps lateral, in which case the record would not show the initiation of the mechanical response; and fourthly, the surrounding muscles and tissues may tend to obscure the actual beginning of the response. In physiological studies with lower animal forms the executant muscle can be isolated and freed from such surrounding tissues, but this is obviously impossible in working with human subjects. It is perhaps not possible to eliminate entirely or even to reduce further the influence of

these extraneous factors in a comparative study such as has been here attempted. Consequently, although the latent time of the muscle is probably a large factor in explaining the difference between the two latent times in a given case, it is not valid to assume that the difference is a true measure of the latent time of the muscle.

Range of the differences between the latencies for the two techniques. It was to be expected that the differences between the latencies as measured by the two techniques would show some variation from case to case, due perhaps to the individual variations in the actual latent time of the muscle. A supplementary explanation can be offered to account for a part of the rather large

TABLE VII. *Effect of moving the electrodes on time relations between latencies as recorded by the two techniques in patellar reflex (differences between latencies in σ).*

Subject	Electrode on motor point	Electrode 1" proximal to motor point	Electrode 1" distal to motor point
1	12.7	13.0	11.8
2	11.7	12.0	14.3
3	12.6	11.8	15.0
4	11.1	12.0	13.3
5	10.3	11.6	13.9

spread found. Dodge (4) has shown that in using the muscle-thickening technique the latent time varies greatly with the point on the muscle from which the record is taken. Evidence to support this finding was obtained in this study. Table VII shows the results of a set of check experiments carried out to show that placing the electrodes does affect the time relationships between the latencies as recorded by the two techniques. Differences between the latencies were found to vary as much as 3.5 σ when the electrodes were moved only one inch from the calculated motor point. The fact that the range of the differences is greater for the Achilles than for the patellar reflex supports this suggestion that part of the variation of the differences from case to case is due to the placing of the electrodes, for as Travis and Young (17) have pointed out, the measurements for the locating of the motor point are probably less reliable for the Achilles than for the patellar reflex.

Relation of the action-current volley to the duration of the mechanical response. Buchanan (1) has pointed out that in the frog the mechanical effect outlasts the electrical effect. In fact the latter is often over before the former has reached its maximum. This was found to be true in the human being as well. Fig. 3 shows quite clearly that the action-current volley and the mechanical response of the muscle are not co-extensive. Table VIII gives the interval from the striking of the tendon to the beginning of the mechanical response and from the striking of the tendon to the end of the action-current volley. The difference between these two measures shows how long the action-current volley continued after the mechanical effect had begun. Since the action-current volley is consistently much shorter in the

TABLE VIII. *Overlap of the electrical and of the mechanical responses in Achilles and patellar tendon reflexes (in σ).*

Reflex	From signal to beginning of mechanical response	From signal to end of action-current volley	Overlap of electrical and mechanical response
Achilles	40.7	49.3	8.6
Patellar	31.1	48.2	17.1

Achilles than in the patellar reflex, the overlap is only about one-half as long for the former as for the latter, being 8.6 σ in the Achilles reflex and 17.1 σ in the patellar reflex.

The duration of the mechanical response of the muscle could not be measured with any degree of accuracy in the records obtained in this study, because the alternating current generator used to record the muscle-thickening latencies did not follow the form of the thickening. Dodge (4) states that in the patellar reflex the rising phase of the mechanical response occupies about 50.0 σ , and that the contraction continues about 100.0 σ , making a total of 150.0 σ , after which the curve begins to fall. Figures published by Rounds (12) indicate that the total Achilles response is probably somewhat shorter, lasting about 120 σ . If we assume that the mechanical response probably begins about 5.5 σ sooner than our figures show it will be found that the electrical response overlaps the mechanical response by about 15.0 σ in the Achilles reflex and by about 25.0 σ in the patellar reflex. Thus the action-

current volley is co-existent with the mechanical response for only about one-eighth of the duration of the latter in the Achilles reflex and for about one-sixth in the patellar reflex. This would seem to lend support to the theory advanced by *Fulton* (9) that the electrical response, or the action current, is caused by the wave of altered permeability which passes over the muscle at the arrival of the nerve impulse, while the mechanical response, or the muscle thickening, is caused by the actual contraction of the muscle fibers.

Interval between the signal and the first mechanical twitch of the muscle. Inasmuch as many of the workers using the muscle-thickening technique for recording the latent times in both the Achilles and the patellar reflexes (*e.g.*, *Dodge*, *Miles*, *Rounds*) have used the beginning of the first mechanical movement of the

TABLE IX. *Average interval of time elapsing between the striking of the tendon and the first mechanical movement of the muscle in the Achilles and patellar reflexes (in σ).*

Reflex	Average interval	S.D.
Achilles.....	5.4	.588
Patellar.....	4.2	.431

muscle as the signal indicating the application of the stimulus, it is of interest to note that in our records an interval of from 4–5 σ elapsed from the actual striking of the tendon to the appearance of this movement. Table IX shows the average time for this interval in both the Achilles and patellar reflexes. While it is probable that the first mechanical movement, caused by the stretching of the muscle by the blow on the tendon, indicates the actual moment of stimulation of the end organs in the muscle initiating the reflex, the records indicate that from 4.0–5.5 σ should be added to the latent times obtained by the muscle-thickening technique if the first mechanical twitch of the muscle is used to determine the time of stimulation; or, conversely, 4.0–5.5 σ should be subtracted from the times obtained by either the muscle-thickening or the action-current techniques if the moment of striking of the tendon is recorded as the moment of stimulation. A measure of the reflex latency from the actual stimulation of the muscle end organs to the arrival of the nerve impulses

initiating the wave of altered permeability (the probable cause of the action currents) may be obtained by subtracting from 4.0–5.5 σ from the latencies obtained by the action-current technique.

IV. Summary and conclusions. 1. By means of a Westinghouse portable oscillograph and an alternating electrical current generator records of the action-current and muscle-thickening response latencies were obtained from a group of 30 adults for the Achilles reflex and for 29 adults for the patellar reflex. Both latencies were recorded simultaneously on a single film and both were read from the same time- and signal-line. From 25–50 consecutive records of the reflex elicitations were obtained from five subjects in both the Achilles and the patellar reflexes, as well as records both before and after fatigue of the gastrocnemius muscle in two subjects.

2. For the Achilles reflex a correlation of $.80 \pm .043$ and for the patellar reflex, a correlation of $.78 \pm .054$ were obtained between the response latencies determined by the action-current technique and those determined by the muscle-thickening technique. These correlations are regarded as being sufficiently high to warrant the conclusion that the two techniques give measures of reflex response latency that are dependent on the same or closely related factors.

3. An essentially constant relationship was shown to exist between the latencies as obtained by the use of the two techniques, since the range and the standard deviation from the mean for the latencies as obtained by either technique were approximately the same in each individual case. This is taken to indicate that for comparative purposes either technique would be satisfactory if carefully controlled and refined.

4. The essentially constant relationship found to exist between the latencies as obtained by the two techniques holds true for a long as well as a short series of consecutive measures. For this reason a short series (6–10) of elicitations was sufficient to determine the latency by either technique.

5. Peripheral fatigue of the gastrocnemius muscle apparently

had no effect on the reflex response latency as measured by either technique.

6. The latency of the executant muscle as measured by finding the difference between the action-current latency and the muscle-thickening latency in any given case was found in the Achilles reflex to be 11.8σ , in a range of $8.1-17.5 \sigma$, and in the patellar reflex, 12.6σ , in a range of $10.2-15.1 \sigma$. In the light of findings by *Fulton*, *Sherrington* and others, these measures must be regarded as probably somewhat too long to be the actual latencies of the muscle involved. Several extraneous and probably uncontrollable factors were mentioned that would serve to obscure the actual initiation of the muscle response. These factors further suggest that the action-current technique is more refined than the muscle-thickening technique for the recording of reflex response latencies.

7. The cessation of the action-current volley before the mechanical response of the muscle has run its full course, the former having often terminated before the muscle thickening had reached its maximum, tends to support the theory advanced by *Fulton* (9) that the electrical response is caused by a wave of altered permeability passing over the muscle when it is stimulated by the innervating nerve impulse, while the mechanical response is caused by the actual contraction and consequent shortening of the muscle fibers.

8. An interval of from $4-5 \sigma$ was found to intervene between the striking of the tendon and the first mechanical movement of the muscle caused by its being stretched from the blow on the tendon.

Bibliography

1. BUCHANAN, F. The relation of the electrical to the mechanical reflex response in the frog, *Quart. J. Exper. Physiol.*, 5, 1912, 91-130.
2. BURDON-SANDERSON, J. Photographic determination of the time relation of the changes which take place in muscle during the period of so-called "latent stimulation," *Proc. Roy. Soc.*, 48, 1890, 14-19.
3. BURDON-SANDERSON, J. The electrical response to stimulation of muscle and its relation to the mechanical response, *J. Physiol.*, 18, 1895, 117-159.
4. DODGE, R. A systematic exploration of a normal knee-jerk, its technique, the form of muscle contraction, its latent time, and its theory, *Zeits. f. allg. Physiol.*, 12, 1911, 1-58.

5. DODGE, R., and BENEDICT, F. S. Psychological effects of alcohol: an experimental investigation of the effects of moderate doses of ethyl alcohol on a related group of neuromuscular processes in man, *Carnegie Instit. Pub.*, No. 232, 1915.
6. EINTHOVEN, W. The relation of mechanical and electrical phenomena of muscular contraction, with special reference to the cardiac muscle, The Harvey Lectures, Series XX. Philadelphia: Lippincott, 1924-25.
7. ERLANGER, J., and GASSER, H. The compound nature of the action current of nerve as disclosed by the cathode ray oscillograph, *Amer. J. Physiol.*, 70, 1924, 624-666.
8. FEARING, F. Reflex action. Baltimore: Williams and Wilkins, 1930.
9. FULTON, J. F. Muscular contraction and reflex control. Baltimore: Williams and Wilkins, 1926.
10. MCLEOD, J. J. Physiology and biochemistry in modern medicine. St. Louis: C. V. Mosby, 1930.
11. MILES, W. Alcohol and human efficiency, *Carnegie Instit. Pub.*, No. 333, Washington, 1924.
12. ROUNDS, G. Is the latent time in the Achilles tendon reflex a criterion of speed in mental reactions?, *Arch. Psychol.*, No. 95, 1928.
13. ROYAL, T. A study of the latent time of the intact gastrocnemius muscle of man (M.A. thesis, Univ. of Iowa), 1932.
14. SHERRINGTON, C. The integrative action of the nervous system. New Haven: Yale Univ. Press; London: Humphrey Milford, 1923.
15. TRAVIS, L., and HUNTER, T. Tremor frequencies, *J. Gen. Psychol.*, 5, 1931, 255-260.
16. TRAVIS, L., and HUNTER, T. The relation between intelligence and reflex conduction rate, *J. Exper. Psychol.*, 11, 1928, 342-354.
17. TRAVIS, L., and YOUNG, C. The relations of electromyographically measured reflex times in the patellar and Achilles reflexes to certain physical measurements and to intelligence, *J. Gen. Psychol.*, 3, 1930, 374-399.
18. TRAVIS, L., and DORSEY, J. Effect of alcohol on the patellar tendon reflex time, *Archiv. Neur. and Psychiat.*, 21, 1929, 613-624.
19. TUTTLE, W. An apparatus for eliciting and recording the patellar tendon reflex time, *Amer. J. Physiol.*, 68, 1924, 338-344.
20. TUTTLE, W., TRAVIS, L., and HUNTER, T. A study of the reflex time of the knee-jerk and the Achilles-jerk, *Amer. J. Physiol.*, 82, 1927, 99-105.

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